SEASONAL BIOLOGICAL CYCLES IN ATLANTIC COD (Gadus morhua) AND IMPLICATIONS FOR FISHERIES AND MANAGEMENT: A SIMULATION APPROACH WITH APPLICATION TO THE PLACENTIA BAY COD FISHERY (NAFO SUBDIVISION 3Ps)

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Seasonal biological cycles in Atlantic cod (*Gadus morhua*) and implications for fisheries and management: a simulation approach with application to the Placentia Bay cod fishery (NAFO subdivision 3Ps)

by

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Abstract

Atlantic cod (*Gadus morhua*) is a demersal fish found across the North Atlantic Ocean in a variety of habitats from the shoreline to the continental shelf slope. Throughout its range of distribution, cod experience a great variety of biotic and abiotic conditions, particularly in relation to thermal and feeding regimes. Such variations affect life history characteristics such as growth, physiological condition, distribution and migration patterns at a variety of scales including decadal, annual and seasonal. In this study I investigate how these processes vary on a seasonal scale level and affect fisheries, stock assessment and management of cod from Placentia Bay, Newfoundland (Northwest Atlantic Fisheries Organization Subdivision 3Ps). The results of this study show that cod have marked seasonal variability in traits such as weight, physiological condition, growth, distribution and aggregations patterns, in addition to the commercial yield and quality of fish products. These changes were related to changes in thermal and feeding regimes through the year, in addition to spawning, migration and intermixing of cod from different geographic regions. Cod ages 4-9 experienced a rapid increase in weight and condition during late spring and summer when capelin (*Mallotus villosus*) comprised an important component of the diet, despite of cold water temperatures and moderate to high spawning activity and peaked in the fall. Seasonal variations of biological cycles, distribution and mixing of different groups of cod resulted in large within-year variations in stock abundance, age and size composition, impacted fishing levels and harvest rates of putative stock components and affected precision of abundance index estimates. Simulation results suggest that stock performance and productivity are impacted by the

way fishing mortality is distributed across age groups and that stock growth and catch yield are driven by the survival of younger fish and by allowing age diversity in the stock, which appears to facilitate good recruitment, particularly when abundance is high. The simulations show that a weight-based fishery in the fall when cod are heavier and in good physiological condition would harvest fewer fish and result in better yield and product quality. However, a fall fishery would concentrate exploitation on the resident component of the stock. The largest sustainable catches were observed in summer when the most abundant non-resident fish are found in the bay. Overall, the results and conclusions of this thesis suggest that seasonal biological patterns in cod may be used to develop fishing and management strategies that minimize the impact of harvesting on productivity while optimizing economic benefits and conservation of stock components. The results from this study are likely relevant to other cod stocks and perhaps to other species (e.g., invertebrates, marine mammals) as seasonality is a common feature of reproduction and growth of many temperate and high latitude aquatic species, which are normally synchronised with periods when organisms benefit from favourable thermal conditions and high forage status.

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Dedicatory

This thesis is dedicated to my parents, Benedito and Maria, who taught me many valuable principles in life and gave me the opportunity to pursue my wishes and dreams and to my wife and sons, Frances, Neeson and Erik, whose love, patience and smiles kept me going through calm and rough seas and ultimately helped me to succeed. I thank you all from the bottom of my heart.

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Symbol	Description	Unit
	Chapter 2	
c_j	Catch weight landed by the Sentinel fisheries for month *j*	t
C_j	Catch weight landed by the commercial fisheries for month *j*	t
h_i	Liver weight	g
H_0	Null hypothesis	-
HSI	Hepato-somatic index	-
i	Individual fish	number
K	Fulton's condition factor	$g.cm^{-3}$
l_i	total length	cm
n	Number of observations	number
n_j	Number of fish for month *j*	number
n_{aj}	Partial catch at age matrix of age *a* fish for month *j*	number
N_{aj}	Total catch at age matrix of age *a* fish for month *j*	number
P	Probability	-
SD	Standard deviation	kg or -
t_j	Total weight of fish for month *j*	kg
TAC	Total allowable catch	t
w_i	Somatic weight	kg
χ^2	Chi-square statistic	-
r	Pearson product-moment correlation coefficient	-

Chapter 3

β	Regression model coefficient	-
c	Regression coefficient	number
d_j	Gonad weight of cod *j*	g
f	Regression function	number
F_i	Frequency of occurrence	number
GLM	General linear models	-
I_G	Gonado-somatic index	-
I_P	Partial fullness index	$g.cm^{-3}$
I_T	Total fullness index	$g.cm^{-3}$
l_j	Length of cod *j*	cm
m_j	Somatic weight of cod *j*	g
n	Number of observations	number
n_i	Number of stomachs containing the prey group *i*	number
N	Number of non-empty stomachs	number
$o_{j,k}$	Offset	g
p_j	Weight of a prey group for cod *j*	g
P	Probability	-
$r_{j,k}$	growth rate of cod *j* in day *k*	-
SD	Standard deviation	^0C or -
T_A	Ambient temperature	^0C
x_k	Predictor or independent variable	g
X_i	Values of predictors	$g.cm^{-3}$, ^0C or -

y_k	Predicted mean somatic weight at day *k* for cod age *a*	g
Y_i	Dependent variable	-
ε_k	Random error	number

Chapter 4

a	Range	km
au	Arbitrary unit	-
b	Taylor's power law index	-
c	Sill	$(fish.m^{-2})^2$
CV	Coefficient of variation	-
D	Detectability	-
h	Distance	km
i	Spatial location	degree
I	Inner bay	-
j	Spatial location	degree
k	Negative binomial index	-
N	Number of pair of points in a two-dimensional plan	number
O	Outer bay	-
s_a	Area backscattering coefficient	$m^2.m^{-2}$
TAC	Total allowable catch	t
TS	Target strength	dB
x	Sample in ordinary kriging	$fish.m^{-2}$
z	Fish density	$fish.m^{-2}$
Z(V)	Estimated fish density using kriging	$fish.m^{-2}$

$\gamma(h)$	Variogram model	$(fish.m^{-2})^2$
λ	Kriging model weight used to minimise model variance	-
θ_{bs}	Mean acoustic backscattering cross section of one fish	m^2

Chapter 5

a	Range	km
c	Sill	$(fish.m^{-2})^2$
C1-C3	Cluster centroids	-
CV	Coefficient of variability	-
D	Detectability	-
df	Degrees of freedom	number
GSI	Gonado-somatic index	-
h	Distance	km
HSI	Hepato-somatic index	-
I	Inner bay	-
K	Fulton's condition factor	$g.cm^{-3}$
n	number of observations	number
N	Number of pair of points in a two-dimensional plan	number
O	Outer bay	-
P	Probability	-
s_a	Area backscattering coefficient	$m^2.m^{-2}$
SD	Standard deviation	$fish.m^{-2}$
TS	Target strength	dB
wt	Biomass	t

x	Sample in ordinary kriging	$fish.m^{-2}$
z	Fish density	$fish.m^{-2}$
Z(V)	Estimated fish density using kriging	$fish.m^{-2}$
χ^2	Chi-square statistic	-
$\gamma(h)$	Variogram model	$(fish.m^{-2})^2$
λ	Kriging model weight used to minimise model variance	-
Θ_{bs}	Mean acoustic backscattering cross section of one fish	m^2

Chapter 6

a	Fish age	year
b	Catch biomass	t
B	Stock biomass	t
e	base of natural logarithm	-
f	Proportion of mature females	-
F_1-F_5	Instantaneous rate of fishing mortality	-
g_a	Number of eggs produced by an age *a* cod	number
h	Harvest rate	-
i(t)	Environmental index at time *t* (water temperature anomaly)	°C
M	Instantaneous rate of natural mortality	-
n	Number of observations	number
n_a	Catch at age	number
N	Stock abundance	number
N_3	Number of recruits	number
$N_{a,0}$	Stock abundance at age *a* at the beginning of the simulations	number

P	Probability	-
p	Survival rate	-
q	Ratio female/male	-
r^2	Coefficient of determination	-
SD	Standard deviation	number or -
S_1-S_5	Simulation scenarios 1 to 5	-
t	Time	year
TAC	Total allowable catch	t
u_a	Catch rate for cod age *a*	-
w_a	Mean total weight of cod age *a*	kg
y	Random number	number

Chapter 1. General Introduction and Thesis Overview

1.1 Introduction

Atlantic cod (*Gadus morhua*, Linnaeus, 1758) is a demersal fish that is widely distributed in a variety of habitats from the shoreline to the continental shelf slope, mostly at depths < 200 m. Cod occur throughout the North Atlantic Ocean from Cape Hatteras (North Carolina, USA) to Baffin Island (Canadian Arctic), along the east and west coasts of Greenland, Iceland, and the coasts of Europe from the Bay of Biscay (France) to the Barents Sea (Cohen *et al.*, 1990).

Cod is a long-lived species attaining ages of 20 years or more and can grow to lengths of 130 cm and weights of up to 35 kg (Fahay *et al.*, 1999). Fecundity is high, with an average production of 1 million eggs per female, with a maximum reported production of 9 million eggs for a 34 kg fish (Cohen *et al.*, 1990). Cod typically spawn from December to June (Brander, 1994) mainly near the bottom in spawning shoals or at times in pelagic spawning columns (Rose, 1993; Morgan *et al.*, 1994; Lawson and Rose, 2000a). Eggs and larva (25-50 mm) are pelagic, but subsequent post-larva move towards the bottom (Fahay, 1983).

Throughout their range of distribution, cod experience a great variety of biotic and abiotic conditions, particularly in relation to thermal and feeding regimes. Such variations affect life history characteristics such as growth rate, physiological condition, distribution and migration patterns of individuals and groups of fish (Nilssen *et al.*, 1994; Dutil *et al.*, 1999; Yaragina and Marshall, 2000). Overall, a

latitudinal cline associated with growth has been observed in cod (Brander, 1995; Krohn *et al.*, 1997). Growth tends to be slower off Labrador and eastern Newfoundland than on the southern Grand Bank and slower in the Gulf of St. Lawrence than on the Scotian Shelf (Scott and Scott, 1988). Similar findings have been reported in the northeast Atlantic, with cod from the English Channel and the North Sea growing faster than those living at higher latitudes (Cohen *et al.*, 1990).

In addition to water temperature, cod growth is dependent also on the quality and quantity of feeding (Scott and Scott, 1988). Cod is considered to be a generalist and opportunistic predator. Diet changes with age, with larva and post-larva feeding on plankton, while juveniles feed mainly on invertebrates and older cod on invertebrates and fish, including young cod (Hop *et al.*, 1992; Link and Garrison, 2002). Small crustaceans comprise a larger proportion of the diet of juvenile cod (< 25 cm), but the consumption of larger invertebrates (e.g., crab, shrimp) tends to increase as cod grow, and fish became more important than invertebrates to the diet of older cod (Link and Garrison, 2002; Rose and O'Driscoll, 2002). In addition, while the consumption of invertebrates may vary little through the year, fish consumption for different cod stocks varies seasonally. For example, Turuk (1968) reported that cod from southern Labrador feed largely on capelin during the fall and winter, while cod from eastern Newfoundland shelf feed on capelin during the winter. Similar findings were reported by Lilly (1991) regarding the fall diet of cod from the southern Labrador Shelf. Hop *et al.* (1992) showed that during the

winter in southern Norway small and large cod feed mainly on large invertebrates and fish, respectively.

Some groups of cod, such as those inhabiting coastal embayments in southern Labrador or Norway are relatively stationary and only undertake small-scale (< 50 km) seasonal migrations (Godø *et al.*, 1986; Green and Wroblewski, 2000; Robichaud and Rose, 2004), while other groups of cod may perform long migrations or occurring in some geographic areas only at specific periods of the year. In the Northwest Atlantic for example, cod off Newfoundland have been observed to undergo seasonal migrations at continental shelf scale associated with reproduction and thermal regimes (Rose, 1993). At the extreme ranges of their distribution cod are only present during the summer and early fall (eastern coast of Labrador) (Turuk, 1968; Templeman, 1979), or winter and spring (Gulf of Maine) (Heyerdahl and Livingstone, 1982; Hunt *et al.*, 1999). Greenland cod have been observed to migrate over distances exceeding 900 km (Rätz, 1994), while cod of the North Sea and Irish Sea undertake migrations of lesser magnitude (Arnold *et al.*, 1994; Turner *et al.*, 2002). Arcto-Norwegian cod spend most of the year in the Barents Sea, but migrate seasonally to the Norwegian coast for spawning (Godø, 1995; Ponomarenko, 1996).

Cod have been exploited for centuries on both sides of the North Atlantic mainly during migratory periods (Templeman, 1979; Brander, 1994; Lear, 1998) and the cod fishery is among the most important of all commercial fisheries, historically

accounting for approximately 30% of the world's total groundfish catch (Cohen, 1990). World catches reported in the FAO Yearbook of Fishery Statistics indicated that over 2 million t of cod were landed in 1987. However, since the early 1990s catches have decreased in more than half, with total landings declining to 944,000 t in 2001. The cod fishery in the northwest Atlantic was the largest with landings varying between 1 and 1.9 million t during the 1950s and late 1960s (Lear, 1998). However, since the 1990s the Northeast Arctic and Icelandic cod fisheries have maintained large annual catches, mostly between 300,000 and 500,000 t (Anon., 2000), with the Northeast Arctic having the largest cod fishery in the world (Yndestad, 2001).

In recent decades, many cod stocks (a stock is defined here as a management unit, while a population is defined as a group of fish whose spawning is isolated from other populations), including those in Atlantic Canada (FRCC, 2003a; 2003b; and 2003c), Greenland, Iceland, the Baltic and North Seas (Brander, 1994; Anon., 2000) have declined to low abundance levels and resulting in the collapse of some stocks and the announcement of fishing moratoria (Myers *et al.,* 1997; Rätz, 1997; Fu *et al.*, 2001a). In the northwest Atlantic, the factors believed to have contributed to the decline of the cod stocks include overfishing (Hutchings and Myers, 1994; Myers *et al.*, 1997), or the combined effects of overfishing and environmental factors (colder environmental conditions during the 1980's and 1990's) (Dutil *et al.*, 1999; Rose *et al.*, 2000; Rice, 2002). In some cases, uncertainties related to the effect of cod biological cycles (e.g., intermix of

different stocks during feeding periods) on abundance estimations (from fishery statistics and research survey data) or on the effectiveness of management strategies may also have contributed to stock decline (Walters and Maguire, 1996; Myers *et al.*, 1997).

Seasonal variability in growth, physiological state, reproductive cycle, distribution and migration have been observed in most cod stocks in Atlantic Canada (Rose, 1993; Lambert and Dutil, 1997; Lilly, 1998; Dutil *et al.*, 1999) and throughout the North Atlantic (Daan, 1974; Jangaard *et al.*, 1967; Eliaseen and Vahl, 1982; Yaragina and Marshall, 2000; Lloret and Rätz, 2000). Furthermore, cod found in fishing areas may undergo changes in size, age, or gender composition, as the result of ontogenetic, reproductive or feeding cycles (Swain, 1993; Rose, 1993; Lawson and Rose, 2000b; Robichaud, 2001). In addition, many other species inhabiting temperate and high latitude environments like invertebrates and marine mammals experience periodic variability in biological traits (Serchuk and Smolowitz, 1989; Nilssen et al., 1997; Brokington and Clarke, 2001) as seasonality is a common feature of reproduction, growth and migratory cycles, which are normally synchronised with periods when organisms benefit from favourable thermal conditions and high forage status. Such variability may potentially result in changes of stock biomass and economic yields of commercial fisheries of cod and other species (e.g., harvest rates, product quality and yield) over the annual cycle (Anderson, 1989; Larkin and Sylvia, 1999; Schwalme and Chouirnard, 1999; Fu et al., 2001b). Seasonal distribution and life history variants

may also affect the capacity of assessment methods to estimate abundance and hence make catch projections, which could lead to conservation concerns. For example, fishing during periods when fish are in poor physiological condition, or when the available stock is comprised of a larger proportion of small fish may result not only in loss of economic yield, but also in jeopardy to the stock, through harvesting more fish to attain a weight-based quota.

Although many aspects of the seasonal biology of cod have been studied, few studies have attempted to link biological cycles to the quality and market value of cod (Bjarnason, 1995; Schwalme and Chouinard, 1999). Furthermore, no attempts have been made to develop harvesting strategies (e.g., timing of fishing) that optimise seasonal harvest in relation to biological cycles, economic benefits and stock conservation. In addition, the effect of seasonal patterns of distribution and growth on abundance estimates is largely unknown. This thesis will attempt to address some of these questions using the inshore cod fishery in Placentia Bay (Northwest Atlantic Fisheries Organization subdivision 3Ps) as an example. Placentia Bay is located on the south coast of Newfoundland and currently is the centre of the largest cod fishery in the Northwest Atlantic. Historical catches from Placentia Bay are not known. However, the proportion of cod caught in the bay during 1999-2000 reached up to 50% of the total 3Ps landings (Brattey *et al.*, 2003). Total reported landings in 3Ps declined from 59,000 t in 1987 to 36,000 t in 1992 and a moratorium on cod fishing was imposed in August 1993 after 15,000 t had been landed. The fishery remained closed until May 1997. Since the fishery

reopened, total allowable catch (TAC) has ranged between 10,000 t and 30,000 t, and currently is 15,000 t (FRCC, 2003a).

Specifically, the objectives of this study are (1) to describe the seasonal patterns of physiological condition and growth of Placentia Bay cod (ages 4-9) for the years 1997-2000; (2) to link the data described in (1) to temporally and spatially corresponding commercial data on landings, yield and product quality; (3) to investigate through simulations how seasonal changes in cod biological cycles may affect stock state (i.e., abundance, growth and recruitment potential) and (4) to propose harvesting strategies that would decrease the impact of fishing on stock productivity while considering economic benefits and conservation concerns.

The working hypothesis of this thesis could be stated as: *seasonal biological patterns in cod may be used to develop fishing and management strategies that minimize the impact of harvesting on stock productivity while optimizing economic benefits and conservation concerns.*

1.2 Thesis overview

Analyses in this thesis are based on data collected during seasonal surveys. The more complete of these surveys, those including both comprehensive acoustic and biological data sets (October and November 1998, April, May, July, October and November 1999 and May 2000) were collected as part of directed research

conducted by the author. These surveys used the same research vessel (except the April trip), echosounder and acoustic sampling design and areas in the main year of the study (1999). Data from the other trips were acquired by former students and researchers of the Fisheries Conservation Chair (Marine Institute, MUN). Acoustic data from trips other than those designed by the author have not been used, as survey design, acoustic equipment and vessel were not comparable. However biological data from these trips are incorporated in Chapters 2 & 3 as biological sampling protocols were similar. In chapters 4, 5 & 6 I emphasise the acoustic data from 1999 due to problems with the echosounder hardware and incomplete sampling due to logistical constraints in 1998 and 2000 (although acoustic estimates for these trips are presented as well). Analysis of acoustic and biological data were limited to cod ages 4-9 in all chapters due to the scarcity of fish caught outside this age range in all surveys. Details on data selection are presented as part of the methodology in each chapter.

The various aspects of cod seasonal biology and implications for fisheries and management are addressed in chapters 2 to 6. Specifically, chapter 2 deals with seasonal cycles in weight and condition in Atlantic cod and here I attempt to quantify through simulations the influence of cycles on stock productivity and economic yield to the fishery in Placentia Bay. In chapter 3, I quantify the effects of water temperature, feeding and reproduction on cod growth. In chapter 4 I investigate the use of geostatistical methods to quantify fish aggregation patterns over a range of spatial scales, using simulated and acoustic density data of Atlantic

cod. I also examine how changes in aggregation patterns may influence the precision of abundance indices. In chapter 5 I quantify seasonal changes in stock abundance resulting from variations in age and size composition, fish condition and spatial dynamics of cod over the annual cycle, assess the impact of current fishing levels on putative stock components and estimate harvest rates during the different fishing seasons. Finally, in chapter 6 I combine all the findings of the previous chapters into a simulation of the Atlantic cod fisheries of Placentia Bay and evaluate the effects of various harvest strategies.

Overall, the findings of each chapter (research papers) are discussed and put into a broader perspective regarding the applicability of the approaches developed in this thesis to other cod stocks and when applicable in the context of other exploited species inhabiting temperate ecosystems.

1.3 Co-authorship statement

All aspects related to design and identification of the research proposal were carried out by the thesis author. I conducted all data analyses. Cod stomach contents analysis was done by Susan Fudge and Bruce Nolan. Ages were determined by otolith reading done by Norman Batten. The thesis author wrote all thesis chapters. Dr. G.A. Rose (supervisor) provided valuable advice on all aspects of the research and on the content of the chapters and is a co-author of all manuscripts.

1.4 References

Anderson, L.G. 1989. Optimal intra- and interseasonal harvesting strategies when prices vary with individual size. Marine Resource Economics, 6: 145-162.

Anon., 2000. Review of the stocks. ICES Advisory Committee on Fishery Management (ACFM). Fish Stock Assessment Working and Study Group Report (2000).

Arnold, G.P., Walker, M.G., Emerson, L.S., and Holford, B.H. 1994. Movements of cod (*Gadus morhua* L.) in relation to the tidal streams in the southern North Sea. ICES Journal of Marine Science, 51: 207-232.

Bjarnason, J. 1995. Seasonal variation in quality of cod. Temanord no. 612.

Brander, K.M. 1995. The effect of temperature on growth of Atlantic cod (*Gadus morhua* L.). ICES Journal of Marine Science, 52: 1-10.

Brander, K.M. 1994. Spawning and life history information for North Atlantic cod stocks. ICES Cooperative Research Report No. 205.

Brattey, J., Cadigan, N.G., Healey, B.P., Lilly, G.R., Murphy, E.F., Stansbury, D.E., and Mahé, J.-C. 2003. An assessment of the cod (*Gadus morhua*) stock in

NAFO Subdivision 3Ps in October 2003. DFO Canadian Stock Assessment Secretariat Research Document 2003/092.

Brokington, S., and Clarke, A. 2001. The relative influence of temperature and food on the metabolism of a marine invertebrate. Journal of Experimental Marine Biology and Ecology, 258: 87-99.

Cohen, D.M., Inada, T., Iwamoto, T., and Scialabba, N. 1990. Gadiform fishes of the world (Order Gadiformes). An annotated and illustrated catalogue of cods, hakes, grenadiers and other gadiform fishes known to date. FAO Species Catalogue No. 125, Vol. 10. Rome, FAO. 1990.

Daan, N. 1974. Growth of north seas cod, *Gadus morhua*. Netherlands Journal of Seas Research, 8: 27-48.

Dutil, J.-D., Castonguay, M., Gilbert, D., and Gascon, D. 1999. Growth, condition, and environmental relationships in Atlantic cod (*Gadus morhua*) in the northern Gulf of St. Lawrence and implications for management strategies in the Northwest Atlantic. Canadian Journal of Fisheries and Aquatic Sciences, 56: 1818-1831.

Eliassen, J.E., and Vahl, O. 1982. Seasonal variations in biochemical compositions and energy content of liver, gonad and muscle of mature and immature cod, *Gadus*

morhua (L.) from Balsfjorden, northern Norway. Journal of Fish Biology, 20: 707-716.

Fahay, M.P., Berrien, P.L., Johnson, D.L., and Morse, W.W. 1999. Atlantic cod, *Gadus morhua*, life history and habitat characteristics. NOAA Technical Memorandum NMFS-NE-124.

Fahay, M.P. 1983. Guide to the early stages of marine fishes occurring in the western North Atlantic Ocean, Cape Hatteras to the southern Scotian Shelf. Journal of the Northwest Atlantic Fishery Science, 4: 1-423.

FRCC (Fisheries Resource Conservation Council), 2003a. 2003/2004 conservation requirements for groundfish stocks on the Scotian Shelf and in the Bay of Fundy (4VWX5Z), in Sub-areas 0, 2+3 and redfish stocks. Report to the Minister, FRCC. 2003, R.1, January 2003.

FRCC (Fisheries Resource Conservation Council), 2003b. 2003/2004 conservation requirements for 2J3KL cod stocks. Report to the Minister, FRCC. 2003, R.2, March 2003.

FRCC (Fisheries Resource Conservation Council), 2003c. 2003/2004 conservation requirements for groundfish stocks in the Gulf of St. Lawrence. Report to the Minister, FRCC. 2003, R.3, April 2003.

Fu, C., Mohn, R., and Fanning, L.P. 2001a. Why the Atlantic cod (*Gadus morhua*) stock off eastern Nova Scotia has not recovered. Canadian Journal of Fisheries and Aquatic Sciences, 58: 1613-1623.

Fu, C., Quinn, T.J., II, and Shirley, T.C. 2001b. The role of sex change, growth and mortality in *Pandalus* population dynamics and management. ICES Journal of Marine Science, 58: 607-621.

Green, J.M., and Wroblewski, J.S. 2000. Movement patterns of Atlantic cod in Gilbert Bay, Labrador: evidence for bay residency and spawning site fidelity. Journal of the Marine Biological Association of the United Kingdom, 80: 1077-1085.

Godø, O.R. 1995. Transplantation-tagging-experiments in preliminary studies of migration of cod off Norway. ICES Journal of Marine Science, 52: 955-962.

Godø, O.R., Halland, T.I., and Agotnes, P. 1986. Tagging experiment results on cod in Western Norway fjord areas. ICES C.M. 1986 (G80).

Heyerdahl, E.G., and Livingstone, R. 1982. Atlantic cod, *Gadus morhua*. *In* M.D. Grosslein and T.R. Azarovitz (eds.). Fish distribution. p. 70-72. MESA New York Bight Atlas Monograph 15. N.Y. Sea Grant Institute, Albany, N.Y.

Hop, H., Gjøsæter, J., and Danielssen, D.S. 1992. Seasonal feeding ecology of cod (*Gadus morhua* L.) on the Norwegian Skagerrak coast. ICES Journal of Marine Science, 49:453-461.

Hunt, J.J., Stobo, W.T., and Almeida, F. 1999. Movement of Atlantic cod, *Gadus morhua*, tagged in the Gulf of Maine area. Fishery Bulletin, 97: 842-860.

Hutchings , J.A., and Myers, R.A. 1994. What can be learned from the collapse of a renewable resource? Atlantic cod, *Gadus morhua*, of Newfoundland and Labrador. Canadian Journal of Fisheries and Aquatic Sciences, 51: 2126-2146.

Jangaard, P. M., Brockerhoff, H., Burgher R.D., and Hoyle R.J. 1967. Seasonal changes in general condition and lipid content of cod from inshore waters. Journal of the Fisheries Research Board of Canada, 24: 607-612.

Krohn, M., Reidy, S., and Kerr, S. 1997. Bioenergetic analysis of the effects of temperature and prey availability on growth and condition of northern cod (*Gadus morhua*). Canadian Journal of Fisheries and Aquatic Sciences, 54: 113-121.

Lambert, Y., and Dutil, J.D. 1997. Condition and energy reserves of Atlantic cod (*Gadus morhua*) during the collapse of the northern Gulf of St. Lawrence stock. Canadian Journal of Fisheries and Aquatic Sciences, 54: 2388-2400.

Larkin, S.L., and Sylvia, G. 1999. Intrinsic fish characteristics and intra-season production efficiency: a management-level bioeconomic analysis of a commercial fishery. American Journal of Agricultural Economics, 81:29-43.

Lawson, G.L., and Rose, G.A. 2000a. Small-scale spatial and temporal patterns in spawning of Atlantic cod (*Gadus morhua*) in coastal Newfoundland waters. Canadian Journal of Fisheries and Aquatic Sciences, 57: 1011-1024.

Lawson, G.L., and Rose, G.A. 2000b. Seasonal distribution and movements of coastal cod (*Gadus morhua*) in Placentia Bay, Newfoundland. Fisheries Research, 49: 61-75.

Lear, W.H. 1998. History of fisheries in the Northwest Atlantic: The 500-year perspective. Journal of Northwest Atlantic Fisheries Science, 23: 41-73.

Lilly, G. R. 1998. Size-at-age and condition of cod in Subdivision 3Ps as determined from research bottom-trawl surveys (1972-1997). Canadian Stock Assessment Secretariat Research Document 98/94.

Lilly, G.R. 1991. Interannual variability in predation by cod (*Gadus morhua*) on capelin (*Mallotus villosus*) and other prey off southern Labrador and northeastern Newfoundland. ICES Marine Science Symposium, 193: 133-146.

Link, J.S., and Garrison, L.P. 2002. Trophic ecology of Atlantic cod *Gadus morhua* on the northeast US continental shelf. Marine Ecology Progress Series, 227: 109-123.

Lloret, J., and Rätz, H.J. 2000. Condition of cod (*Gadus morhua*) off Greenland during 1982-98. Fisheries Research, 48: 79-86.

Morgan, M.J., Deblois, E.M., and Rose, G.A. 1994. An observation on the reaction of Atlantic cod (*Gadus morhua*) in a spawning shoal to bottom trawling. Canadian Journal of Fisheries and Aquatic Sciences, 54: 217-223.

Morris, C.J., and Green J.M. 2002. Biological characteristics of a resident population of Atlantic cod (*Gadus morhua* L.) in southern Labrador. ICES Journal of Marine Science, 59: 666-678.

Myers, R.A., Hutchings, J.A., and Barrowman, N.J. 1997. Why do fish stocks collapse? The example of cod in Atlantic Canada. Ecological Applications, 7: 91-106.

Nilssen, K.T., Haug, T., Grotnes, P.E., and Potelov, V. 1997. Seasonal variation in body condition of adult Barents Sea harp seals (*Phoca groenlandica*). Journal of the Northwest Atlantic Fishery Science, 22: 17-25.

Nilssen, E.M., Pedersen, T., Hopkins, C.C.E., Thyholt, K., and Pope, J.G. 1994. Recruitment variability and growth of Northeast Arctic cod: Influence of physical environment, demography, and predator-prey energetics. ICES Marine Science Symposia, 198: 449-470.

Ponomarenko, V.P. 1996. Distribution of mature cod, *Gadus morhua morhua* of the Barents Sea in relation to seasonal variation in the maturity of gonads. Journal of Ichthyology, 36: 385-390.

Rätz, H.-J. 1997. The development of the Atlantic cod off Greenland during the second half of the 20th century. Informationen fur die Fischwirtschaft, 44: 3-9.

Rätz, H.-J. 1994. Assessment of the migration of Atlantic cod (*Gadus morhua* L.) between the stocks off West and East Greenland in 1984-86 by means of otolith typing. Journal of the Northwest Atlantic Fishery Science, 16: 7-18.

Rice, J. 2002. Changes to the large marine ecosystem of the Newfoundland-Labrador Shelf. *In* Large marine ecosystems of the North Atlantic. Changing states and sustainability, pp. 51-103. Ed. By K Sherman and S.R. Skjoldal. Elsevier Science, London.

Robichaud, D., and Rose, G.A. 2004. Migratory behaviour and range in Atlantic cod: inference from a century of tagging. Fish and Fisheries, 5: 1-31.

Robichaud, D. 2001. Homing, population structure and management of Atlantic cod (*Gadus morhua*) with emphasis on spawning at Bar Haven in Placentia Bay, Newfoundland. Ph.D. thesis, Memorial University of Newfoundland, St. John's, NL.

Rose , G.A., and O'Driscoll, R.L. 2002. Capelin are good for cod: can the northern stock rebuild without them? ICES Journal of Marine Science, 59: 1018-1026.

Rose, G.A., de Young, B., Kulka, D.W., Goddard, S.V., and Fletcher, G.L. 2000. Distribution shifts and overfishing the northern cod (*Gadus morhua*): a view from the ocean. Canadian Journal of Fisheries and Aquatic Sciences, 57: 644-663.

Rose, G.A. 1993. Cod spawning on a migratory highway in the northwest Atlantic. Nature, 366: 458-461.

Schwalme, K., and Chouinard, G.A. 1999. Seasonal dynamics in feeding, organ weights, and reproductive maturation of Atlantic cod (*Gadus morhua*) in the southern Gulf of St. Lawrence. ICES Journal of Marine Science, 56: 303-319.

Scott, W.B., and Scott, M.G. 1988. Atlantic fishes of Canada. Canadian Bulletin of Fisheries and Aquatic Sciences No. 219.

Serchuk, F.M., and Smolowitz, R.J. 1989. Seasonality in sea scallop somatic growth and reproductive cycles. Journal of Shellfish Research, vol. 8, p 435.

Swain, D.P. 1993. Age- and density-dependent bathymetric pattern of Atlantic cod (*Gadus morhua*) in the southern Gulf of St. Lawrence. Canadian Journal of Fisheries and Aquatic Sciences, 50: 1255-1264.

Templeman, W. 1979. Migration and intermingling of stocks of Atlantic cod, *Gadus morhua*, of the Newfoundland and adjacent areas from tagging in 1962-66. ICNAF Research Bulletin, 14: 5-50.

Turner, K., Righton, D., and Metcalfe, J.D. 2002. The dispersal patterns and behaviour of North Sea cod (*Gadus morhua*) studied using electronic data storage tags. Hydrobiologia, 483: 201-208.

Turuk, T.N. 1968. Seasonal changes of cod feeding in the Labrador and Newfoundland areas in 1964 - 1966. TRUDY PINRO, 23: 370-382.

Waters, C, and Maguire, J.J. 1996. Lessons for stock assessment from the northern cod collapse. Reviews in Fish Biology and Fisheries, 6:125-137.

Yaragina, N.A., and Marshall, C.T. 2000. Trophic influences on inter-annual and seasonal variation in the liver condition index of Northeast Arctic cod (*Gadus morhua*). ICES Journal of Marine Science, 57: 42-55.

Yndestad, H. 2001. Earth nutation influence on Northeast Arctic cod management. ICES Journal of Marine Science, 58: 799-805.

Chapter 2 Seasonal cycles in weight and condition in Atlantic cod (*Gadus morhua* L.) in relation to fisheries

2.1 Abstract

Weight and physiological condition of Atlantic cod (*Gadus morhua*) ages 4 to 9 sampled in Placentia Bay, Newfoundland, between 1997 and 2000 showed strong seasonal variability and influenced productivity and economic impacts of the fishery. Condition indices (Fulton's K condition factor and hepato-somatic index - HSI) were lowest during the spawning season (spring) and increased rapidly during the post-spawning period, reaching maximum values by fall (K and HSI increased on average 24% and 82% between spring and fall, respectively). Condition indices were correlated with an industry index of product yield. Historically, cod fisheries have been prosecuted during all seasons, but simulations of 1997-1999 fisheries indicate that a fall fishery (period of peak physiological condition) resulted in an annual 8-17% decrease in the number of cod removed from the stock while maintaining the same weight-based quotas and profiting from maximum yield and better product quality. Spring and summer fisheries resulted in lower yield (6%) and quality (7-21%) of fish products by weight. Seasonal biological cycles could be used as templates for management strategies that promote fisheries conservation and economic benefits by harvesting fish during periods when biological impacts are minimal and economic returns maximal

2.2 Introduction

Seasonal variability in weight and physiological condition related to feeding and reproduction has been observed in many fish species inhabiting temperate ecosystems (Schwalme and Chouinard, 1999; Craig *et al.*, 2000; Shulman, 2002). Such variability may influence stock biomass and also the potential economic benefit of fisheries, as a consequence of seasonal changes in yield and quality of fish products (Sylvia *et al.*, 1996; Larkin and Sylvia, 1999). In addition, seasonal weight variability may influence mortality rates in fisheries having weight-based quotas, because fewer fish will be harvested when fish are heavier and in good physiological condition.

Seasonal declines in weight and condition typically occur during reproductive periods as fish use energy for gonad development and spawning behaviour (Cubillos *et al.*, 2001; Lucifora *et al.*, 2002; Shulman, 2002). Nonetheless, many temperate water fisheries are prosecuted on spawning fish (Stephenson, 1997; Rose *et al.*, 2000; Frank and Brickman, 2001). Some studies have linked seasonal variability in fish condition with the quality and market value of harvested fish (Bjarnason, 1995; Schwalme and Chouinard, 1999), but only a few attempts have been made to optimise harvesting strategies (e.g., timing of fishing) in relation to biological cycles or to address the related economic benefits (Larkin and Sylvia, 1999).

In this study I investigate the seasonality of weight and condition in an Atlantic cod (*Gadus morhua*) inshore fishery in southern Newfoundland. In particular, I (1) describe

and quantify the effect of seasonality in weight and condition on the fishery and economic properties of harvested cod, (2) examine through simulation the effect of harvest timing on potential catch weight and (3) investigate seasonal harvesting regimes that optimise stock productivity, conservation and economic benefits.

2.3 Material and Methods

2.3.1 Area of study

This study was conducted in Placentia Bay, a large and highly featured embayment situated on the south coast of Newfoundland (Northwest Atlantic Fisheries Organization subdivision 3Ps, hereafter 3Ps) (Figure 2.1). The inner bay is divided by a series of islands into three deep channels that merge to form a basin (outer bay) that extends from the bay to the continental shelf. Placentia Bay remains ice-free year-round, except for areas near strong fresh water inflows. Depths reach 450 m in the channels. The bottom topography is rugged and variable (Willey, 1976), particularly in the inner bay.

2.3.2 Fishery

Southern Newfoundland has been a centre for Atlantic cod fisheries since the early 16th century (Lear, 1998). Harvesting of cod has occurred during all seasons using handline, baited long-line, otter trawl cod trap and gillnet (now the dominant gear). Historical catches from Placentia Bay are not known. However, the proportion of cod caught in the

bay during 1999-2000 reached up to 50% of the total 3Ps landings (Brattey *et al.*, 2003). Total reported landings in 3Ps declined from 59,000 t in 1987 to 36,000 t in 1992 and a moratorium on cod fishing was imposed in August 1993 after 15,000 t had been landed. The fishery remained closed until May 1997. Since the fishery reopened, total allowable catch (TAC) has ranged between 10,000 t and 30,000 t, and currently is 15,000 t (FRCC, 2003).

2.3.3 Biological data

Cod in Placentia Bay were sampled during 24 acoustic surveys conducted between January 1997 and June 2000 (Table 2.1). Eighteen surveys were conducted from small research vessels (10-25 m) employing a calibrated BioSonics DT 4000 echosounder (Foote *et al.*, 1987) with 38 and 120 kHz transducers mounted on a towed body. Biological sampling on these vessels was conducted with handlines (depth of capture < 60 m), using four lines each having six equal size unbaited hooks (10.2 cm long by 2.6 cm wide) for 30 minutes. The remaining surveys were conducted using a research trawler (63 m) equipped with a calibrated Simrad EK 500 echosounder with a hull-mounted 38 kHz transducer. Biological samples were taken with a Campelen 1800 bottom trawl fished at 3.5 knots for 15 minutes (depth of capture < 100 m). In all cases fish were caught on or near the bottom.

Fishing was directed at acoustically identified cod aggregations and for most surveys, fishing sets were conducted in both inner and outer bay (Table 2.1). A total of 5665 fish

(ages 4-9) were sampled for total length, total weight, somatic weight (total weight – organ weight), liver weight, sex, maturity stage and otolith for age determination. Cod length and weight were measured to the nearest cm and g, respectively. Spawning fish were identified using the visual classification criteria provided by Morrison (1990). Spawning females had hydrated eggs in their ovaries, and spawning males had distended, opaque to white gonads exuding running milt in most cases. Age determination was done by Norm Batten (Department of Fisheries and Oceans, St. John's, Newfoundland) and consisted in the reading of concentric dark and light rings (each pair = one year) observed in the cross section of a sagitae otolith of cod.

Although fish were captured using two different gears, it was assumed that the selectivity in terms of weight at age was comparable, as neither gear selected by fish girth. In addition, there is the possibility of selectivity by handline towards actively feeding fish, which could confound seasonal patterns in weight or condition. However, cod are avid predators and have been shown to feed during most periods of the year when prey is available (Turuk, 1968; Hop *et al.*, 1992; Schwalme and Chouinard, 1999). Therefore, sampling bias towards actively feeding fish is not likely to be a concern in this study.

For each survey, Fulton's K condition factor and hepato-somatic index (HSI) were calculated as $K_i = [(w_i / l_i^3) \times 100]$ and $HSI_i = (h_i / w_i)$, where w_i is the somatic weight (g), l_i is total length (cm) and h_i is the liver weight (g) of cod i. K and HSI are considered to describe the physiological state of Atlantic cod (Lambert and Dutil, 1997). For each

survey and age group, mean somatic weight, K and HSI were estimated from the overall number of fish caught in all fishing sets.

2.3.4 Industry data

Data on yield and quality of cod during July 1998 and December 2000 were obtained from processing records at the National Sea Products (NSP) plant in Arnold's Cove, Placentia Bay. The catch processed by NSP comprised approximately half of the total commercial catches in Placentia Bay during the study period (N. Bolt, personal communication). The data include estimates of package yield and two product quality indices, block % and grade A % for the overall catch processed monthly by NSP. Package yield is defined as the weight of the processed fillets divided by the weight of the raw material (gutted fish). Block % is the proportion (by weight) of total fillets not suitable for premium product and packed into block frames. Grade A % is the proportion of the total fillets (by weight) classified as grade A. Grade A fillets have firm muscle texture, no bruising and white colour. Seasonal variability was expressed as the percentage difference between the monthly and annual means.

2.3.5 Simulation

Simulations were used to examine the effect of harvest timing on potential landings. For each year, two scenarios were considered. In the first scenario (A) the simulated stock was harvested with the same seasonal pattern as observed in the commercial cod fishery

in Placentia Bay (1997-1999), while in scenario B the fishery was restricted to periods when cod condition was high (half of the catch was allowed to occur in November and the other half in December). Since monthly catch at age data from the commercial fishery were not available for this study (E. Murphy, personal communication), monthly catch at age numbers and biomass were derived using a combination of data which were available. This included monthly catch weight (t) for the Placentia Bay fishery (Stansbury *et al.*, 1998; Brattey *et al.*, 1999 and 2000), monthly length frequency data (Appendix 2.1) from the sentinel fishery catch by gillnets (R. Stead, personal communication) and measurements of length, weight and age from the survey sampling. A partial catch at age matrix ($n_{a,j}$) was calculated for each year and month using length frequencies from the sentinel fishery catch and monthly age-length keys derived from acoustic survey data and then scaled to the total monthly catch at age ($N_{a,j}$) harvested by the fishery and calculated as $N_{a,j} = n_{a,j} \times (C_j / c_j)$ and $c_j = (\sum_{\text{age groups}} (n_{a,j} \times t_{a,j}))$, where C_j and c_j are the total catch weight for the commercial and sentinel fisheries, respectively, n_j is the number of fish (from age-length keys) and t_j is the average total weight of cod age a for month j estimated from acoustic surveys. The simulated total catch weight was projected by summing the products of each month's catch at age ($N_{a,j}$) by t_j.

2.3.6 Statistical analyses

Variations in mean somatic weight, K and HSI were compared over the years, months and year x month interactions (H_0: no differences among years and months). In most cases data failed the assumptions of normality and homoscedasticity and hence a non-

parametric test was employed (Kruskal-Wallis test). Pearson product-moment correlation was used to measure the association between fish condition and industry variables (H_0: no correlation). For all tests, the significance level was set at 5% ($P < 0.05$).

2.4 Results

2.4.1 Weight

The mean somatic weight differed significantly among months for all ages and among years for ages 6-9 and there were significant interaction terms for ages 5-6 indicating that for these ages seasonal cycles varied among years (Table 2.2). Mean somatic weight varied from 0.6 kg (n = 53, SD = 0.1 kg) for age 4 (1993 cohort in 1997) to 3.2 kg (n = 22, SD = 1.1 kg) for age 9 (1990 cohort in 1999) (Figure 2.2a). Weight tended to decline during April-May and increase towards October-November. The amplitude of this cycle appears strongest in the older fish. For example, the somatic weight of 7 year old cod (1991 cohort) averaged 2.4 kg (n = 56, SD = 0.7 kg) in November 1998 but decreased to 1.9 kg (n = 28, SD = 0.6 kg) in April 1999, a 21% decrease in weight in five months. Considerable weight gains were also observed. The mean weight of 6 year old fish (1993 cohort) increased from 1.3 kg (n = 123, SD = 0.3 kg) in June 1999 to 2 kg (n = 84, SD = 0.4 kg) by November 1999 (54% increase in five months).

2.4.2 Condition

Mean K and HSI differed significantly among months for all ages and among years for age 8 in the case of K and ages 5-8 for HSI and both indices had significant interaction terms for most ages (Table 2.2). Mean K varied from 0.66 $g.cm^{-3}$ (n = 22, SD = 0.04 $g.cm^{-3}$) for age 8 (1992 cohort in 2000) to 0.85 $g.cm^{-3}$ (n = 65, SD = 0.06 $g.cm^{-3}$) for age 4 (1993 cohort in 1997) (Figure 2.2b). Mean HSI varied from 0.02 (n = 14, SD = 0.01) for age 9 (1991 cohort in 2000) to 0.09 (n = 28, SD = 0.01) for age 4 fish in 1997 (Figure 2.2c). A rapid increase in K and HSI was observed during April-June (average increase of 19% and 50%, respectively), peaking in October or November for most cohorts (average increase of 24% and 82% between April and November, respectively) prior to a decline during January. K and HSI values were generally lowest in April.

2.4.3 Spawning

Spawning in Placentia Bay was observed primarily during April-May, although low intensity spawning was also observed at other times of the year (Figure 2.2d). For the most part, the main spawning events coincided with the period when somatic weight was low and K and HSI were near their annual minimal. Inter-annual differences in spawning intensity were pronounced with 1998 having greater spawning activity than the other years.

2.4.4 Length composition

The length composition of the fish sampled with handline during July and November surveys showed significant differences in both 1998 (χ^2= 78.4, n = 554, P < 0.001) and 1999 (χ^2= 132.5, n = 446, P < 0.001). The July catches tended to include a greater proportion of smaller fish while the November catches included larger fish (Figure 2.3).

2.4.5 Industry data

Commercial package yield was lower in spring and higher in fall in both 1999 and 2000 (Figure 2.4a). The overall inter-seasonal variation in yield was approximately 6%. In contrast, block % was in most cases below the annual average (up to 11%) during the fall (1999-2000) and winter (2000) and highest (10-16% above the annual average) in September in both years (Figure 2.4b). The maximum inter-seasonal difference was 21%. The percentage of cod processed as grade A% was above the annual average (up to 7%) from June to December (1998-2000) but below (up to 9%) during spring (1999) and winter (2000) (Figure 2.4c). Package yield was positively correlated with K (r = 0.91, n = 6, P = 0.0007) and HSI (r = 0.88, n = 6, P = 0.001). No significant correlations were detected between condition indices and block % or grade A %.

2.4.6 Simulations

The catch at age data which were used to start the simulations ($N_{a,j}$) show that cod ages 6-8 predominated in the Placentia Bay fishery during 1997-1999 (Figure 2.5). The 1990 cohort (age 7 in 1997) contributed most to the catch in 1997 and the 1992 cohort in 1998 and 1999 (ages 6 and 7 respectively), although by 1999 cod ages 3-5 comprised a sizeable component of the fall catch. The temporal fishing patterns show that the fishery was prosecuted in two main periods, during summer (34-76% of the total catch) and fall (22-63%), although the May-June catch in 1997 comprised up to 42% of the total catch. January to April catches were almost nil in all years as the directed fishery was closed during these periods.

The simulated catch weight from a fishery prosecuted with the same seasonal pattern as the real fishery (scenario A) differed only by 1-7% from the reported catch (Brattey *et al.*, 2003) and indicated that catch increased on average 37% between 1997 and 1998 and 63% between 1998 and 1999 (Table 2.3). The estimated total number of fish caught was approximately 2.3, 3.3 and 4.6 million fish in 1997, 1998 and 1999, respectively. In scenario B (same catch biomass as in scenario A but harvesting occurred during times of peak condition in November-December) resulted in an 8-17% decrease in the number of cod removed from the stock (1.9, 3.1 and 4.2 million fish). This scenario resulted in an additional 403,000, 257,000 and 369,000 fish remaining in the water during 1997-1999 respectively. Under scenario B and an assumption that the additional surviving fish experienced an annual age-independent natural mortality rate of 20%, by the beginning of

2000 the stock would potentially have gained an additional 668,000 fish, which is equivalent to 2,560 t and roughly equivalent to 30% of the total reported catch weight (8,774 t) in Placentia Bay in that year (Brattey *et al.*, 2003).

2.5 Discussion

The analyses indicate that cod condition (K and HSI) varied significantly among seasons for all ages studied (4-9) and show strong correlation with package yield. Cod were in poorest condition in April-May during spawning when yield was lowest. Following spawning, cod feed intensively (Mello and Rose, 2005a), resulting in a considerable and rapid increase in condition during July. By October-November cod were in top condition and yield peaked. Although no significant correlations with K and HSI were detected, block % and grade A% appear to be associated with fish condition at least in some periods. Block % was mostly below the annual average during the fall, whereas the opposite was observed for grade A%, indicating an increase in the proportion of high quality fish being processed during the fall. These findings are similar to seasonal condition cycles reported by Schwalme and Chouinard (1999) for an adjacent cod stock in the southern Gulf of St. Lawrence. These authors speculated that condition would influence the yield of marketable product but offered no industry data.

The results of this study would indicate that if the fishery were to be managed based on seasonal cycles in weight it would be best to have a fall fishery. A fall fishery would catch cod when somatic weight and condition are highest, hence decreasing total

removals. However, harvesting strategies cannot be based solely on seasonal cycles in weight and fish condition, but must also consider temporal variation in abundance, logistical and market factors. In Placentia Bay, in summertime post-spawning cod disperse through the outer bay and beyond while, at times more abundant non-resident cod migrate into the bay, mixing with the local fish and leaving the bay towards the end of summer or beginning of the fall (Templeman, 1979; Davis *et al.*, 1994; Lawson and Rose, 2000; Mello and Rose, 2005b). Consequently a fall fishery would concentrate exploitation on the resident component of the stock. Likewise, a spring fishery would also target resident fish, while they are at their lowest condition, removing a larger proportion of spawning fish and reducing the reproductive potential of the resident fish. In contrast, a summer fishery might target both stock components, including the more abundant migrants. However, the age (size) composition of the stock and fishing patterns during the different seasons suggest that a summer fishery is likely to catch a higher proportion of small fish and decreasing profitability.

The simulations indicated that if the 1997-1999 fisheries had been prosecuted during fall the cod stock in Placentia Bay could have been increased by 2,560 t at the beginning of 2000. From a logistical perspective a temporally constrained fishery strategy could have negative impacts on small boat fishermen, as they are least able to fish during rougher fall weather. There is also a danger of overloading fish plant capacity. However, given that during the study period 70-72% and 79-88% of the total catch by weigh in Placentia Bay occurred in only 3 and 4 months, these issues do not appear to be a deterrent at present. In fact, a contracted fishery is at present the norm in Placentia Bay (Brattey *et al.*, 2001,

2002 and 2003). A benefit of a contracted fall fishery would be that total income per fisherman would likely increase (given the same TAC and assuming that there is no major seasonal difference in the cost of fishing), as a higher proportion of top quality fish in the catch should translate into higher prices to fishers for raw product. Harvesting a larger proportion of fish in fall has the potential to simultaneously optimise harvesting, conservation aspects and economic return. However, such strategy could deplete the resident stock. Hence, a fall fishing strategy would require management at the smaller scale of the Placentia Bay stock. Clearly any management plan must consider all of these factors.

In this study fish weight and condition data used in the simulations were estimated primarily using handline catches. Although the fishery largely used gillnets (gillnets comprised 83-95% of the total catch weight during the study period), it is not expect these gear differences to have affected results. Both gears have similar selectivity for fish 60-80 cm (Cadigan and Brattey, 2000), which comprises the range of sizes of most cod caught in Placentia Bay during surveys and by commercial gillneters (Parsons and Stead, 2003). Selectivity may be an issue with smaller fish as handlining has a higher selectivity for fish < 55 cm (total length) than does gillnetting (Cadigan and Brattey, 2000). It is acknowledged that potential for gear bias may be important when estimating biological characteristics from the data collected using bottom trawl (January and June surveys), but given that the commercial fishery in January was practically nil (< 1% of the total catch was landed in January 1997 through 1999) and only 1-12% in June, it is considered that any such effects would be small.

The results from this study are likely relevant to other cod stocks and perhaps to other species. Seasonal variations in weight and condition have been observed in cod populations from most regions of the North Atlantic, including the Scotian Shelf (Jangaard *et al.*, 1967), the southern and northern Gulf of St. Lawrence (Lambert and Dutil, 1997; Schwalme and Chouinard, 1999) and northern cod (Taggart *et al.*, 1994). In all of these areas, declines in weight and condition occur over the winter. Cod in Greenland (Lloret and Rätz, 2000) and Norwegian waters (Eliassen and Vahl, 1982; Yaragina and Marshall, 2000) show seasonal variations in liver weight. Such patterns suggest that these stocks may experience similar types of variation in biomass, product yield and quality as observed for Placentia Bay cod. The northeast Arctic and Icelandic cod stocks have both been exploited near year-round (Anon., 2000). Hence, in principle, the fisheries on these stocks might also benefit from a harvesting strategy that takes a larger proportion of the catch during periods of peak condition.

Seasonality is a common feature of reproduction and growth of temperate and high latitude aquatic species, which are normally synchronised with periods when organisms benefit from a high forage status (Schultz and Conover, 1997). However, very few marine fishery management plans have attempted to incorporate objectives aimed at optimising harvesting or economic benefits in relation to biological seasonality. Kellogg *et al.* (1988) indicated that the timing of the seasonal North Carolina bay scallop (*Aequipecten irradians* Lamarck) fishery opening had been delayed for several weeks beyond its traditional opening date (a few weeks after the end of the spawning season) based in part on profit and economic efficiency considerations. Similarly, Conrad (1982)

and Anderson (1989) recommended that exploitation strategies of high valued invertebrate fisheries (clams, shrimp and lobster) should consider optimal harvesting periods that take advantage of the growth of the individuals of the stock. This reasoning extends the yield per recruit to a value per recruit approach, which is a common practice used in aquaculture harvesting strategies (McClain and Romaire, 1995; Forsberg, 1999).

The prevailing view in the literature regarding the theory of optimal seasonal harvesting assumes that an increase in harvest value results primarily from seasonal growth in weight (Kellogg *et al.*, 1988; Anderson, 1989; Önal *et al.*, 1991; Fu *et al.*, 2001). However, as this study has shown, higher value may also be related to improvement in the raw product quality (i.e., condition and related flesh composition). Although this principle could be applied to many fisheries, there are few references in the literature. For example, Sylvia *et al.* (1996) and Larkin and Sylvia (1999) used bio-economic models to evaluate the impact of seasonal quality variation of Pacific whiting (*Merluccius productus* Ayres) on optimal management strategies and economic benefits. These studies recommended that a delay in the timing of harvest until the end of the feeding season (historically more than 50% of the annual quota is harvested shortly after the end of the spawning season) would result in more than doubling the net revenue from the fishery because of the improvement of flesh quality.

In conclusion, this study shows that the biological seasonality of cod and possibly of other exploited species in temperate ecosystems may directly influence the harvested quantities of fish and the economics of the fishery, through seasonal variations in product

yield and quality. Furthermore, this study found that condition indices such as Fulton's K condition factor and the hepato-somatic index may be useful in identifying periods of increased stock productivity, yield and quality of fish products. I propose that seasonal biological cycles could be used as templates for management strategies that would promote fisheries conservation and economic benefits by harvesting fish during periods when biological impacts are minimal and economic returns maximal.

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2.7 References

Anderson, L.G. 1989. Optimal intra- and interseasonal harvesting strategies when prices vary with individual size. Marine Resource Economics, 6: 145-162.

Anon. 2000. ICES Fish Stock Assessment Working and Study Group report 2000.

Bjarnason, J. 1995. Seasonal variation in quality of cod. TemaNord, 612: 1-4.

Brattey, J., Cadigan, N.G., Healey, B.P., Lilly, G.R., Murphy, E.F., Stansbury, D.E., and Mahé, J.-C. 2003. An assessment of the cod (*Gadus morhua*) stock in NAFO Subdivision 3Ps in October 2003. DFO Canadian Stock Assessment Secretariat Research Document 2003/092.

Brattey, J., Cadigan, N.G., Healey, B.P., Lilly, G.R., Murphy, E.F., Shelton, P.A., Stansbury, D.E., Morgan, M.J., and Mahé, J.-C. 2002. An assessment of the cod (*Gadus morhua*) stock in NAFO Subdivision 3Ps in October 2002. DFO Canadian Stock Assessment Secretariat Research Document 2002/096.

Brattey, J., Cadigan, N.G., Healey, B.P., Lilly, G.R., Murphy, E.F., Shelton, P.A., Stansbury, D.E., Morgan, M.J., and Mahé, J.-C. 2001. An assessment of the cod (*Gadus morhua*) stock in NAFO Subdivision 3Ps in October 2001. DFO Canadian Stock Assessment Secretariat Research Document 2001/099.

Brattey, J., Cadigan, N.G., Lilly, G.R., Murphy, E.F., Shelton, P.A., and Stansbury, D.E. 2000. An assessment of the cod (*Gadus morhua*) stock in NAFO Subdivision 3Ps in October 2000. DFO Canadian Stock Assessment Secretariat Research Document 2000/134.

Brattey, J., Cadigan, N.G., Lilly, G.R., Murphy, E.F., Shelton, P.A., and Stansbury, D.E. 1999. An assessment of the cod (*Gadus morhua*) stock in NAFO Subdivision 3Ps. DFO Canadian Stock Assessment Secretariat Research Document 99/036.

Cadigan, N., and Brattey, J. 2000. Lower bounds on the exploitation of cod (*Gadus morhua*) in NAFO Divisions 3KL and Subdivision 3Ps during 1997-1999 from tagging experiments. DFO Canadian Stock Assessment Secretariat Research Document 2000/073.

Conrad, J.M. 1982. Management of a multiple cohort fishery: The hard clam in Great South Bay. American Journal of Agricultural Economics, 64: 463-474.

Craig, S.R., MacKenzie, D.S., Jones, G., and Gatlin, III, D.M. 2000. Seasonal changes in the reproductive condition and body composition of free-ranging red drum, *Sciaenops ocellatus*. Aquaculture, 190: 89-102.

Cubillos, L.A., Arcos, D.F., Bucarey, D.A., and Canales, M.T. 2001. Seasonal growth of small pelagic fish off Talcahuano, Chile (37 degree S, 73 degree W): A consequence of

their reproductive strategy to seasonal upwelling? Aquatic Living Resources, 14: 115-124.

Davis, M.B., Lundrigan P., and Ripley, R. 1994. A description of cod stock structure in Placentia Bay, NAFO Subdivision 3Ps. DFO Atlantic Fisheries Research Document 94/032.

Eliassen, J.E., and Vahl, O. 1982. Seasonal variations in biochemical compositions and energy content of liver, gonad and muscle of mature and immature cod, *Gadus morhua* (L.) from Balsfjorden, northern Norway. Journal of Fish Biology, 20: 707-716.

Foote, K.G., Knudsen, H.P., and Vestnes, G. 1987. Calibration of acoustic instruments for fish density estimation: a practical guide. ICES Co-operative Research Report 144.

Forsberg, O.I. 1999. Optimal harvesting of farmed Atlantic salmon at two cohort management strategies and different harvest operation restrictions. Aquaculture Economics & Management, 3: 143-158.

Frank, K.T., and Brickman, D. 2001. Contemporary management issues confronting fisheries science. Journal of Sea Research, 45: 173-187.

FRCC (Fisheries Resource Conservation Council) 2003. 2003/2004 conservation requirements for groundfish stocks on the Scotian Shelf and in the Bay of Fundy

(4VWX5Z), in Sub-areas 0, 2+3 and redfish stocks. Report to the Minister, FRCC. 2003, R.1, January 2003. 120 pp.

Fu, C., Quinn, T.J., II, and Shirley, T.C. 2001. The role of sex change, growth and mortality in *Pandalus* population dynamics and management. ICES Journal of Marine Science, 58: 607-621.

Hop, H., Gjøsæter, J., and Danielssen, D.S. 1992. Seasonal feeding ecology of cod (*Gadus morhua* L.) on the Norwegian Skagerrak coast. ICES Journal of Marine Science, 49: 453-461.

Jangaard, P.M., Brockerhoff, H., Burgher, R.D., and Hoyle, R.J. 1967. Seasonal changes in general condition and lipid content of cod from inshore waters. Journal of the Fisheries Research Board of Canada, 24: 607-612.

Kellogg, R.L., Easley, J.E., and Johnson, T. 1988. Optimal timing of harvest for the North Caroline bay scallop fishery. American Journal of Agricultural Economics, 70: 50-62.

Lambert, Y., and Dutil, J.D. 1997. Condition and energy reserves of Atlantic cod (*Gadus morhua*) during the collapse of the northern Gulf of St. Lawrence stock. Canadian Journal of Fisheries and Aquatic Sciences, 54: 2388-2400.

Larkin, S.L., and Sylvia, G. 1999. Intrinsic fish characteristics and intra-season production efficiency: a management-level bioeconomic analysis of a commercial fishery. American Journal of Agricultural Economics, 81:29-43.

Lawson, G.L., and Rose, G.A. 2000. Seasonal distribution and movements of coastal cod (*Gadus morhua* L.) in Placentia Bay, Newfoundland. Fisheries Research, 49: 61-75.

Lear, W.H. 1998. History of fisheries in the Northwest Atlantic: The 500-year perspective. Journal of Northwest Atlantic Fisheries Organization, 23: 41-73.

Lloret, J., and Rätz, H.J. 2000. Condition of cod (*Gadus morhua*) off Greenland during 1982-98. Fisheries Research, 48: 79-86.

Lucifora, L.O., Menni, R.C., and Escalante, A.H. 2002. Reproductive ecology and abundance of the sand tiger shark, *Carcharias taurus*, from the southwestern Atlantic. ICES Journal of Marine Science, 59: 553-561.

McClain, W.R., and Romaire, R.P. 1995. Management considerations for the production of large procambarid crawfish. Journal of Shellfish Research, 14: 553-559.

Mello, L.G.S., and Rose, G.A. 2005a. Seasonal growth of Atlantic cod (*Gadus morhua* L.): effects of temperature, feeding and reproduction. Journal of Fish Biology, 67: 149-170.

Mello, L.G.S., and Rose, G.A. 2005b. Using geostatistics to quantify seasonal distribution and aggregation patterns of fishes: an example of Atlantic cod (*Gadus morhua*). Canadian Journal of Fisheries and Aquatic Sciences, 62: 659-670.

Morrison, C.M. 1990. Histology of the Atlantic cod, *Gadus morhua*: an atlas. Reproductive tract. Canadian Special Publication in Fisheries and Aquatic Sciences 110.

Önal, H., McCarl, B.A., Griffin, W.L., Matlock, G., and Clark, J. 1991. A bioeconomic analysis of the Texas shrimp fishery and its optimal management. American Journal of Agricultural Economics, 73: 1161-1170.

Parsons, D.M., and Stead, R. 2003. Sentinel surveys 1995-2002: Catch per unit effort in NAFO Subdivision 3Ps. Canadian Science Advisory Secretariat Research Document 2003/021.

Rose, G.A., de Young, B., Kulka, D.W., Goddard, S.V., and Fletcher, G.L. 2000. Distribution shifts and overfishing the northern cod (*Gadus morhua*): a view from the ocean. Canadian Journal of Fisheries and Aquatic Sciences, 57: 644-664.

Schultz, E.T., and Conover, D.O. 1997. Latitudinal differences in somatic energy storage: adaptive responses to seasonality in an estuarine fish (Atherinidae: *Menidia menidia*). Oecologia, 109: 516-529.

Schwalme, K., and Chouinard, G.A. 1999. Seasonal dynamics in feeding, organ weights, and reproductive maturation of Atlantic cod (*Gadus morhua*) in the southern Gulf of St. Lawrence. ICES Journal of Marine Science, 56: 303-319.

Shulman, G.E. 2002. Anchovies of the Azov and the Black Sea: regularities of wintering migrations. Marine Ecology Journal, 1: 67-77.

Stansbury, D.E., Shelton, P.A., Brattey, J., Lilly, G.R., Winters, G., Murphy, E.F., Davis, M.B., and Kulka, D.W. 1998. An assessment of the cod stock in NAFO Subdivision 3Ps. Canadian Stock Assessment Secretariat Research Document 98/019.

Stephenson, R.L. 1997. Successes and failures in the management of Atlantic herring fisheries: do we know why some have collapsed and others survived. *In* World Fisheries Congress. Developing and sustaining world fisheries resources. The state of science and management: 2nd World Fisheries Congress, Brisbane (Australia), 28 Jul-2 Aug 1996, pp 49-54. Ed. by D.A. Hancock, D.C. Smith, A. Grant, and J.P. Beumer. CSIRO Publishing, Brisbane, Qld., Australia.

Sylvia, G., Larkin, S.A., and Morrisey, M. 1996. Intrinsic quality and fisheries management: bio-economic analysis of the Pacific whiting fishery. *In* World Fisheries Congress. Developing and sustaining world fisheries resources. The state of science and management: 2nd World Fisheries Congress, Brisbane (Australia), 28 Jul-2 Aug 1996, pp

600-605. Ed. by D.A. Hancock, D.C. Smith, A. Grant, and J.P. Beumer. CSIRO Publishing, Brisbane, Qld., Australia.

Taggart, C.T., Anderson, J., Bishop, C., Colbourne, E., Hutchings, J., Lilly, G., Morgan, J., Murphy, E., Myers, R., Rose, G.A., and Shelton, P. 1994. Overview of cod stocks, biology, and environment in the Northwest Atlantic region of Newfoundland, with emphasis on northern cod. ICES Marine Science Symposium, 198: 140-157.

Templeman, W. 1979. Migration and intermingling of stocks of Atlantic cod, *Gadus morhua*, of the Newfoundland and adjacent areas from tagging in 1962-66. ICNAF Research Bulletin, 14: 5-50.

Turuk, T.N. 1968. Seasonal changes of cod feeding in the Labrador and Newfoundland areas in 1964 - 1966. TRUDY PINRO, 23: 370-382.

Willey, J.D. 1976. Geochemistry and environmental implications of the superficial sediments in northern Placentia Bay, Newfoundland. Canadian Journal of Earth Sciences, 13:1393-1410.

Yaragina, N.A., and Marshall, C.T. 2000. Trophic influences on inter-annual and seasonal variation in the liver condition index of Northeast Arctic cod (*Gadus morhua*). ICES Journal of Marine Science, 57: 42-55.

2.8 Tables

Table 2.1 Number of cod ages 4-9 sampled, gear type and the number of fishing sets per stratum during acoustic surveys in Placentia Bay. T = bottom trawl, and L = handline.

Date		No. fish	Gear	No. fishing sets	
Year	Date	sampled		Inner bay	Outer bay
1997	14-16 Jan	206	T	2	1
	6-12 Apr	178	L	3	2
	21-30 Jun	270	L	3	10
	6-12 Aug	160	L	9	7
	27-29 Sep	74	L	5	4
	4-22 Nov	191	L	10	6
1998	6-8 Jan	482	T	4	2
	14-19 Apr	191	L	0	3
	11-28 May	82	L	3	2
	19-22 Jun	557	T	2	5
	1-5 Jul	234	L	2	0
	10-14 Sep	24	L	1	0
	22-30 Oct	170	L	8	3
	2-27 Nov	350	L	26	4
1999	14-15 Jan	166	T	3	1
	7-22 Apr	373	L	7	5
	4-22 May	117	L	6	3
	2-5 Jun	682	T	3	5
	15-27 Jul	220	L	6	9
	22-30 Oct	134	L	2	1
	2-30 Nov	246	L	10	5
2000	4-7 Apr	100	L	2	1
	5-14 May	106	L	8	7
	6-9 Jun	352	T	2	5
	Total	5,665		127	91

Table 2.2 Results of the Kruskal-Wallis test of temporal patterns in somatic weight, Fulton's condition factor (K) and hepato-somatic index (HSI) of cod ages 4-9 sampled during acoustic surveys in Placentia Bay from January 1997 to June 2000. H = Kruskal-Wallis statistic, df = degrees of freedom, Y = year, M = month, Y x M = interaction term. Superscript ^{NS} = not significant, superscript $^{+}$ = $P < 0.001$, all other cases = $P < 0.0001$.

Age	Source	df	H		
			Weight	K	HSI
4	Model	473	15.1	9.4	13.3
	Y	1	0.3^{NS}	0.01^{NS}	3.1^{NS}
	M	6	27.8	14.8	19.6
	Y x M	5	1.6^{NS}	0.4^{NS}	9.1
5	Model	1 376	44.2	17.5	35.3
	Y	2	2.5^{NS}	0.3^{NS}	18.5
	M	9	67.4	22.1	49.9
	Y x M	11	7.1	2.9	11.2
6	Model	1 452	29.8	14.8	42.1
	Y	3	24.6	2.6^{NS}	20.9
	M	9	31.6	20.7	49.4
	Y x M	13	5.6	4.8	8.6
7	Model	985	13.1	17.4	22.7
	Y	3	5.6	1.9^{NS}	6.9
	M	9	20.7	26.5	28.8
	Y x M	12	2.1^{NS}	2.9	3.2
8	Model	414	6.5	13.9	11.5
	Y	2	11.1	7.6	11.2
	M	8	6.1	11.9	11.4
	Y x M	7	1.4^{NS}	4.6	0.7^{NS}
9	Model	178	7.8	7.5	5.9
	Y	1	17.1	0.2^{NS}	0.01^{NS}
	M	6	4.0^{+}	9.9	8.5
	Y x M	2	3.5^{NS}	1.6^{NS}	3.5^{NS}

Table 2.3 Catch weight (t) and number for simulated cod fishery in Placentia Bay during 1997-1999. Catch weight and number were calculated using monthly catch at age data derived from the sentinel fishery length frequency sampling for gillnets and length-age keys and weight derived from survey data. Reported catch weight for Placentia Bay as in Brattey *et al.* (2003).

Year	Catch weight (t)		Catch number (x 1000)		
	Scenario A	Reported	Scenario A	Scenario B	Difference
1997	5,302	4,956	2,338	1,934	403
1998	7,259	6,991	3,338	3,081	257
1999	11,799	11,654	4,615	4,245	369
Total	24,360	23,601	10,290	9,261	1,029

2.9 Figures

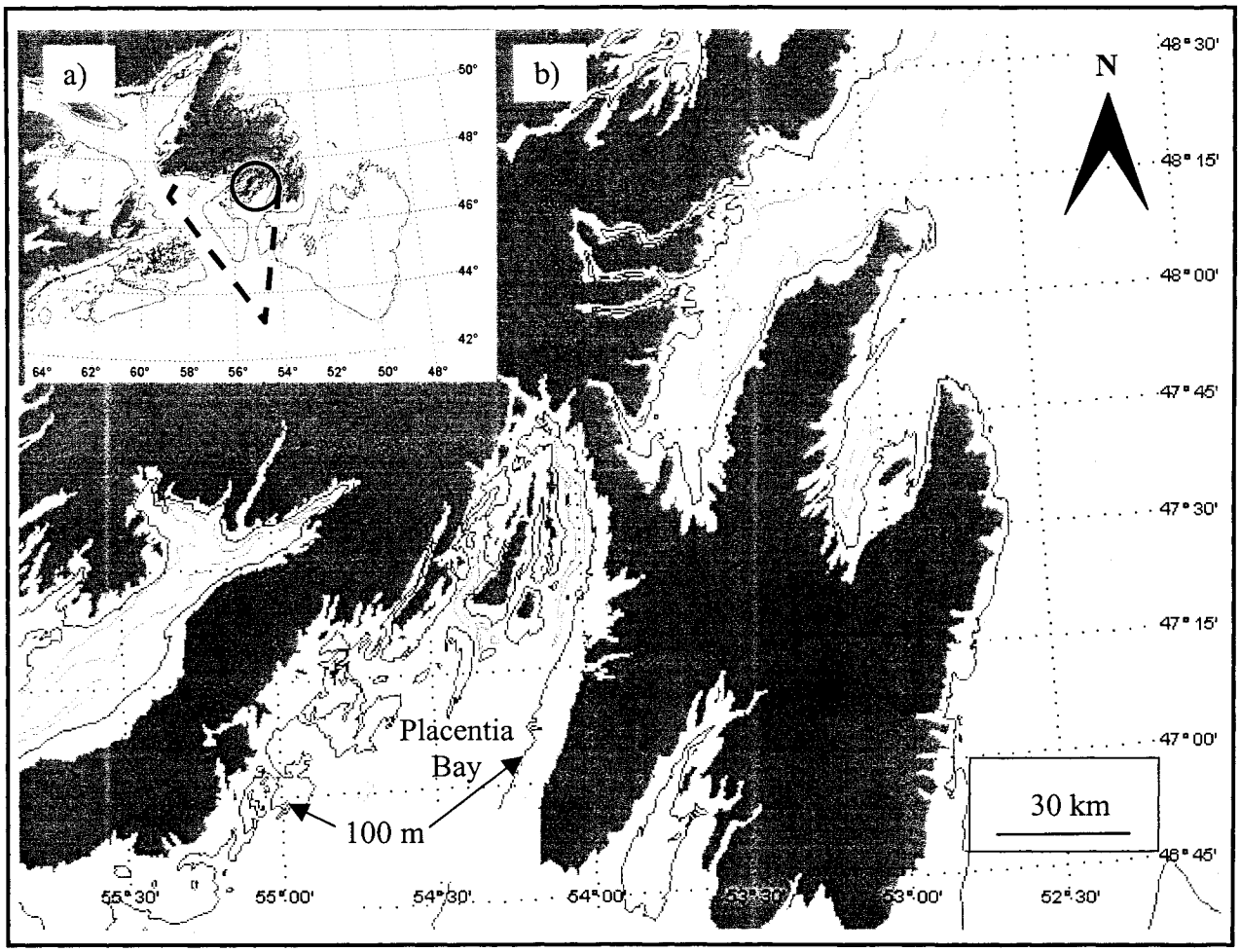

Figure 2.1 (a) East coast of North America showing the Northwest Atlantic Fisheries Organization (NAFO) subdivision 3Ps (dashed line) and Placentia Bay (circle) on the south coast of Newfoundland and (b) detailed view of the bay showing 100 m depth contour (indicated by black arrow).

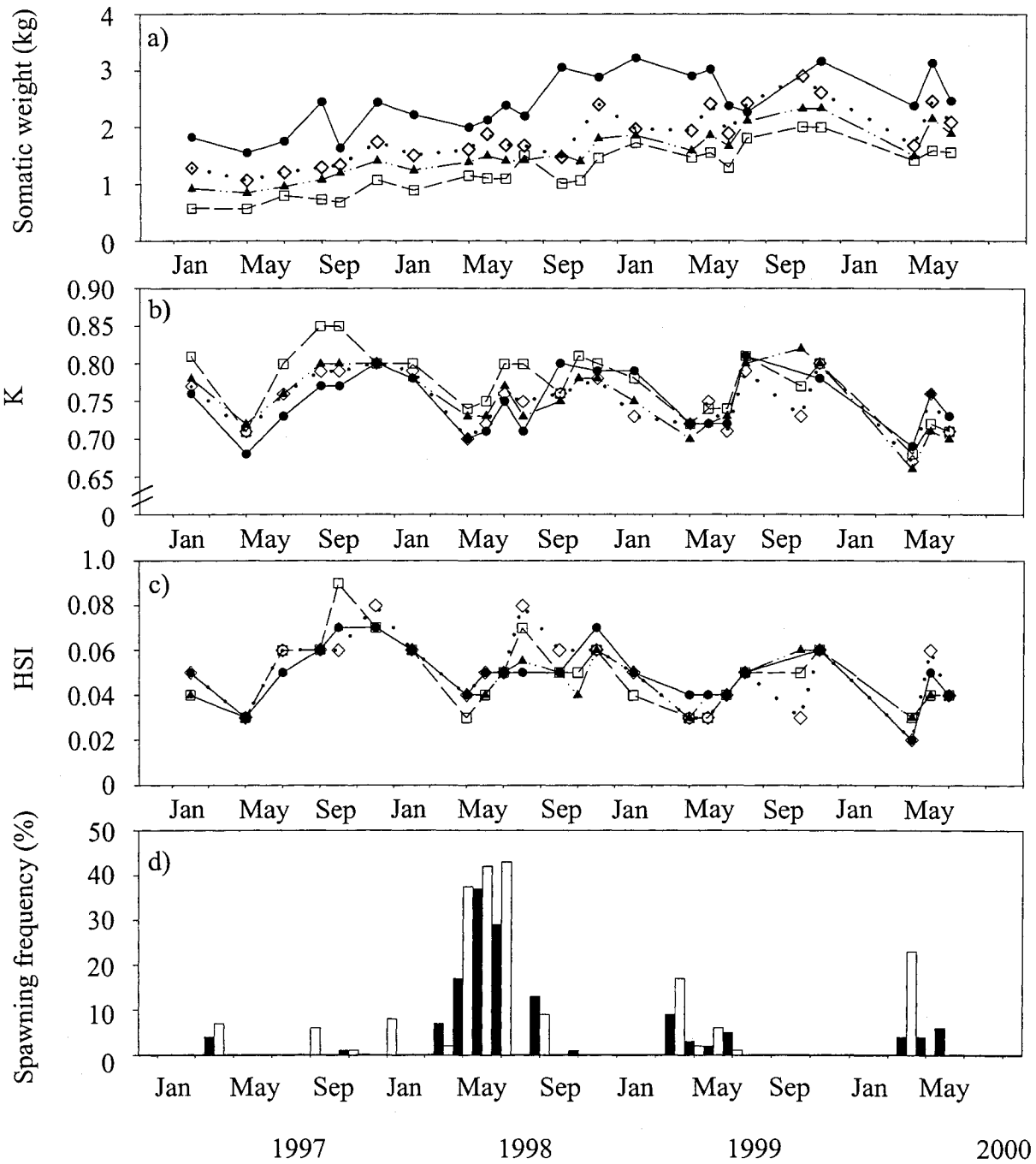

Figure 2.2 (a) Temporal changes in mean somatic weight (kg), Fulton's K condition factor ($g.cm^{-3}$), (c) hepato-somatic index (HSI) and (d) frequency of spawning females (black bar) and males (open bar) from cod sampled during acoustic surveys in Placentia Bay. Cohorts: black circle = 1990, open diamond = 1991, black triangle = 1992 and open square = 1993.

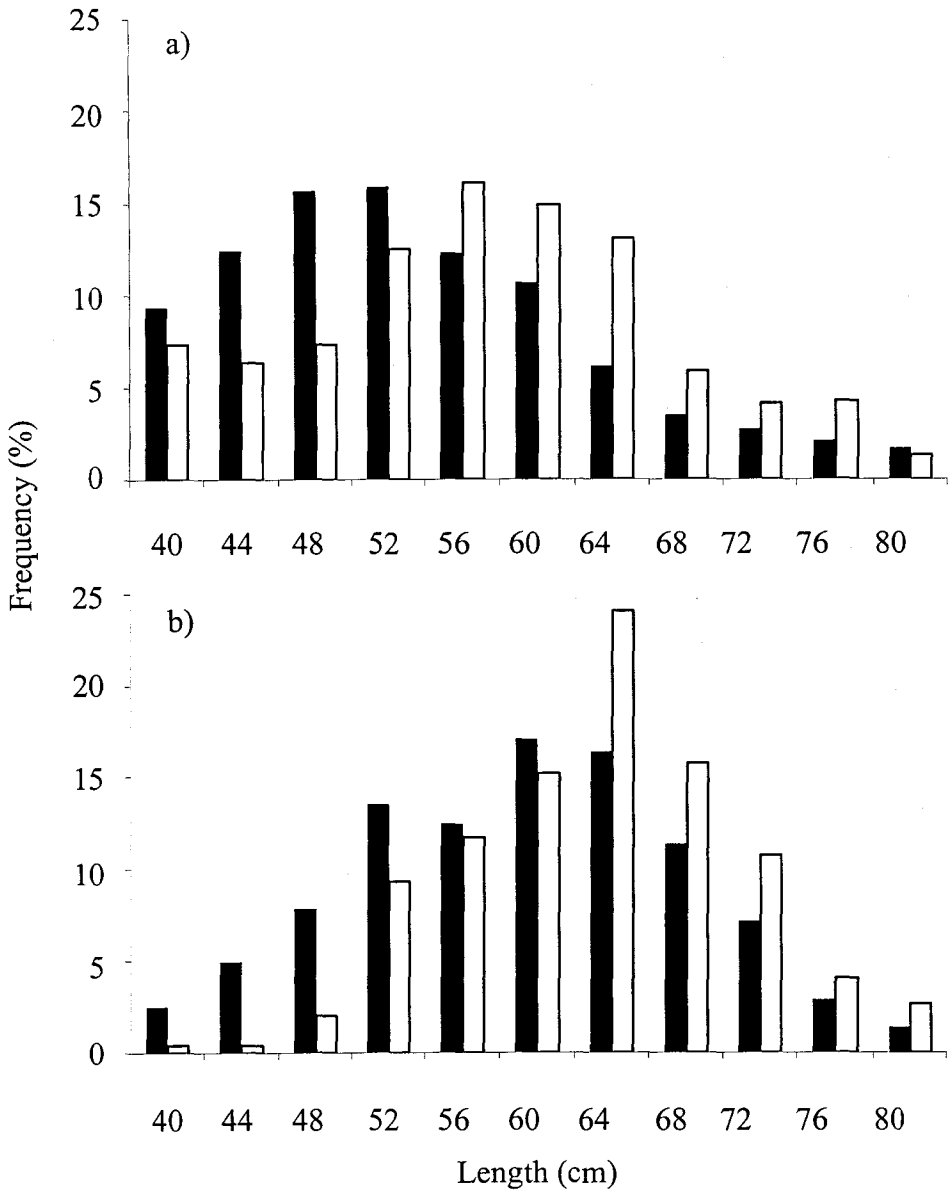

Figure 2.3 Length frequency distribution of cod (40-80 cm) sampled with handline in Placentia Bay during acoustic surveys in July (black bar) and November (open bar) in (a) 1998 (n = 554) and (b) 1999 (n = 446).

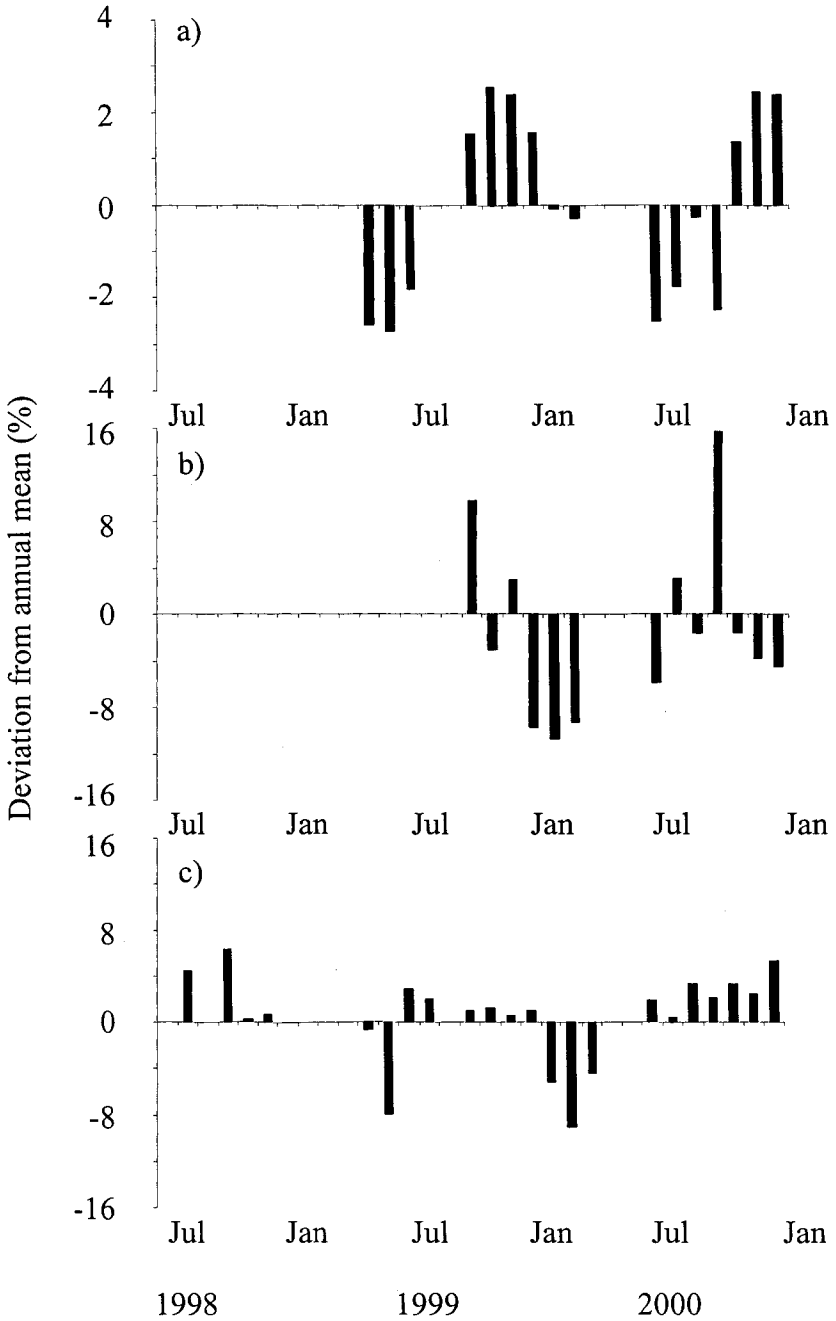

Figure 2.4 Temporal changes in (a) commercial package yield, (b) block % and (c) grade A% from cod processed by National Sea Products fish plant in Arnold's Cove, Newfoundland. Commercial indices are defined in text. Temporal variability is expressed as the percentage difference between the monthly and annual mean indices.

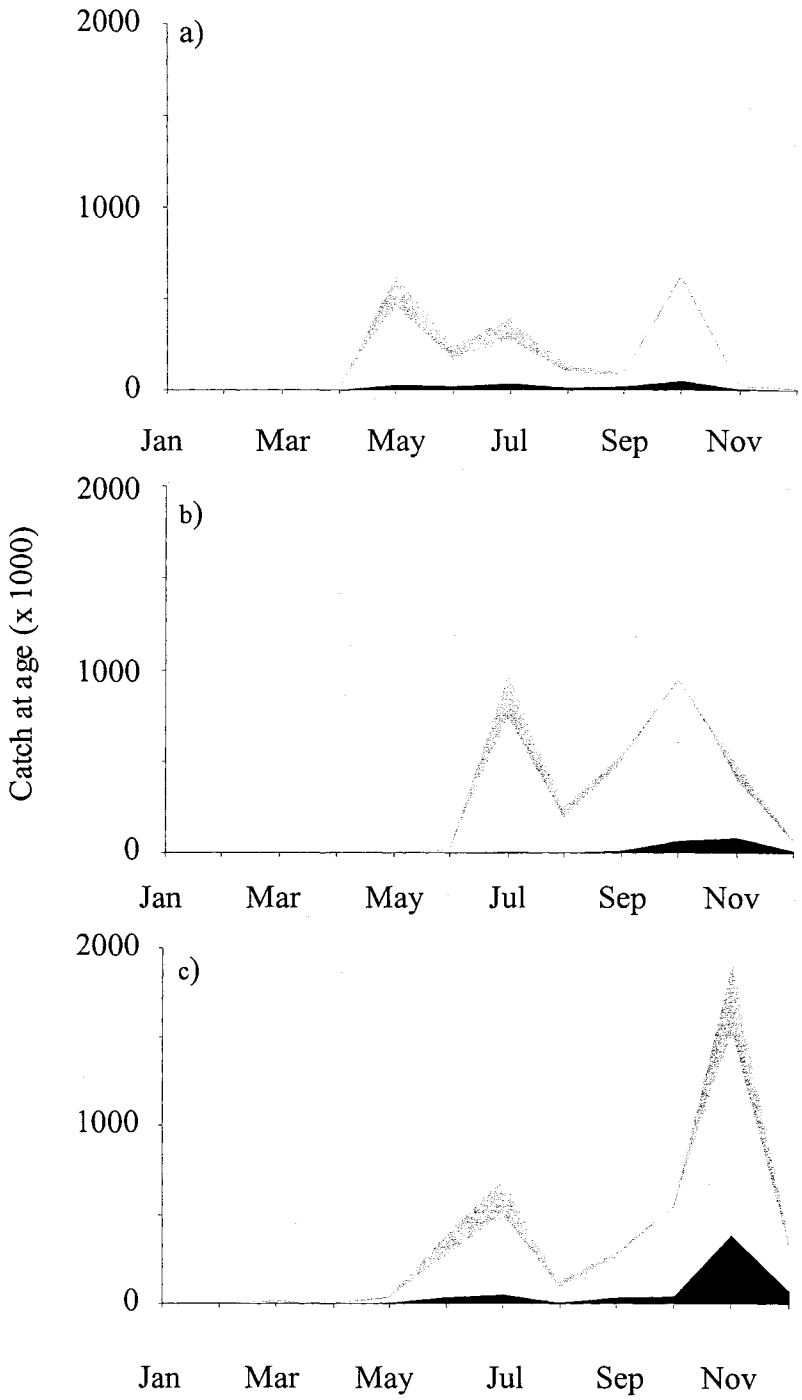

Figure 2.5. Monthly catch at age estimation of the cod fishery in Placentia Bay during (a) 1997, (b) 1998 and (c) 1999, which were used to start the simulations ($N_{a,j}$). Area color: black = ages 3-5, white = ages 6-8 and grey = ages 9-12.

Appendix 2.1 Monthly length frequency distribution (4 cm interval) derived from the sentinel fishery catch by gillnet (mesh size = 14 cm) in Placentia Bay (R. Stead, personal communication).

Year	Length-class (cm)	January	February	March	April	May	June	July	August	September	October	November	December
1997	40	0.01	0.01	0.01	0.01	0.01	0.01	0.02	0.01	0.01	0.05	0.01	0.01
	44	0.01	0	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.02	0.01	0.01
	48	0.04	0.04	0.02	0.05	0.05	0.09	0.08	0.12	0.14	0.07	0.15	0.15
	52	0.05	0.06	0.05	0.05	0.09	0.13	0.13	0.12	0.10	0.37	0.12	0.13
	56	0.41	0.47	0.46	0.40	0.45	0.33	0.31	0.27	0.25	0.39	0.28	0.27
	60	0.30	0.33	0.29	0.31	0.19	0.22	0.18	0.26	0.11	0.01	0.19	0.15
	64	0.02	0.03	0.03	0.02	0.07	0.08	0.07	0.08	0.03	0.01	0.02	0.02
	68	0.08	0	0.08	0.08	0.03	0.09	0.09	0.03	0.09	0	0.01	0.01
	72	0.02	0.01	0.02	0.01	0.04	0.01	0.02	0.01	0.09	0.01	0	0.01
	76	0.04	0.01	0.02	0.03	0.02	0.01	0.05	0.03	0.07	0.02	0.08	0.10
	80	0.02	0.05	0.02	0.05	0.03	0.03	0.04	0.07	0.10	0.05	0.12	0.13
	40	0.01	0.01	0.02	0.01	0.04	0.02	0.07	0.11	0.02	0.02	0.03	0.08
1998	44	0.05	0.01	0.01	0.04	0.01	0.01	0.02	0.03	0.02	0.03	0.02	0.01
	48	0.01	0.02	0.01	0.01	0.10	0.10	0.14	0.01	0.02	0.05	0.15	0.15
	52	0.31	0.29	0.27	0.22	0.28	0.29	0.23	0.27	0.45	0.64	0.19	0.31
	56	0.15	0.16	0.17	0.19	0.16	0.14	0.12	0.11	0.15	0.08	0.23	0.12
	60	0.27	0.23	0.24	0.28	0.21	0.19	0.10	0.12	0.08	0.03	0.18	0.12
	64	0.14	0.14	0.14	0.17	0.14	0.12	0.12	0.14	0.05	0.03	0.12	0.05
	68	0.02	0.03	0.02	0.02	0.02	0.02	0.01	0.01	0.02	0.02	0.02	0.02
	72	0.01	0.05	0.01	0.01	0.03	0.03	0.04	0	0.06	0.06	0.01	0.01
	76	0.03	0.05	0.11	0.01	0.01	0	0.04	0.08	0.11	0.02	0.03	0.05
	80	0.01	0.02	0.01	0.05	0.01	0.08	0.11	0.12	0.02	0.02	0.02	0.08
1999	40	0.05	0.02	0.07	0.09	0.09	0.05	0.01	0.01	0.01	0.03	0.01	0.07
	44	0.01	0.02	0.01	0.01	0.01	0.01	0.01	0.03	0.01	0.02	0.01	0.01
	48	0.02	0.03	0.02	0.03	0.08	0.10	0.07	0.07	0.13	0.05	0.03	0.17
	52	0.20	0.16	0.17	0.14	0.21	0.18	0.25	0.26	0.23	0.31	0.11	0.21
	56	0.26	0.32	0.24	0.23	0.15	0.16	0.16	0.25	0.24	0.34	0.13	0.22
	60	0.28	0.30	0.32	0.27	0.17	0.19	0.21	0.23	0.12	0.01	0.17	0.18
	64	0.09	0.06	0.07	0.09	0.11	0.11	0.14	0.10	0	0.04	0.28	0.03
	68	0.05	0.06	0.05	0.04	0.02	0.05	0.06	0.02	0.07	0	0.14	0.01
	72	0.01	0.01	0.01	0.03	0.03	0.02	0.05	0.01	0.07	0.02	0.08	0.04
	76	0.02	0.01	0.05	0.02	0.06	0.10	0.03	0.01	0.08	0.09	0.02	0.01
	80	0.02	0.01	0	0.05	0.07	0.04	0.01	0	0.05	0.09	0.02	0.05

Chapter 3 Seasonal growth of Atlantic cod (*Gadus morhua*): effects of temperature, feeding and reproduction

3.1 Abstract

Atlantic cod (*Gadus morhua*) experience a great variety of abiotic and biotic conditions throughout the year, particularly in relation to thermal and feeding regimes. Such variations affect life history characteristics at seasonal scales such as growth and reproductive state. Growth rate of cod ages 4-9 examined in Placentia Bay, Newfoundland peaked in most cases in June and was minimum in October or November. Water temperature, partial fullness index (I_P) and gonado-somatic index (I_G) explained between 31-52% of the monthly variability in growth. Temperature and I_P of capelin had both significant effects on growth of most age groups and explained most of the variance for ages 6-8 and 4-5, respectively. The I_P of large invertebrates (ages 4-7), sandlance (*Ammodytes* sp. Reinhardt) (age 6) and demersal fishes (age 9) had age-specific effects. Overall, amphipods, decapods and echinoderms dominated the cod diet in most seasons, but fish consumption by cod was high in June and July, particularly on capelin (*Mallotus villosus* Müller). The rapid increase in somatic weight during June-July occurs despite cold water temperatures (< 2°C at 50 m) and moderate to high gonado-somatic activity. The findings of this study suggest that when food is not a limiting factor (e.g., June), growth tends to increase even when cod occupy colder waters, but when food is limiting, the opposite may occur.

3.2 Introduction

Temperate water organisms typically experience seasonal variations in biotic and abiotic conditions over the annual cycle that affects growth (Bergstedt and Swink, 1995; Chiu and Chen, 2001; Cubillos *et al.*, 2001). In Atlantic cod (*Gadus morhua* L.), water temperature impacts growth directly, through control of metabolic rates and food assimilation (Krohn *et al.*, 1997) and indirectly, by influencing reproduction, feeding and prey availability (Nilssen *et al.*, 1994; Schwalme and Chouinard, 1999). Interactions among these factors may also influence growth and be dependent on fish age, size or abundance (Rose and Leggett, 1990; Swain, 1993). Nevertheless, how such factors are likely to interact and impact growth through the annual cycle has not been well documented (Daan, 1974; Ipatov and Uzars, 1981), despite their possible importance to stock production models and yields and values of seasonal fisheries.

Growth models commonly used in fisheries (e.g., the von Bertalanffy's) may be ineffective at capturing seasonal variations in growth (Coggan, 1997; Essington *et al.*, 2001). Growth in length and weight may be neither isometric nor asymptotic (Shulman, 1974; Gauldie, 1990; Mulligan and Leaman, 1992). Several approaches have been used to measure seasonal variation in fish growth including mark-recapture experiments (Coggan, 1997), otolith annuli reading (Fabré and St. Paul, 1998; Francis *et al.*, 1999), and incorporating empirical functions to isometric or asymptotic growth models (Fontoura and Agostinho, 1996; McGarvey and Fowler, 2002).

The goal of this study was to quantify seasonal variability in somatic weight (total weight – organ weight) of Atlantic cod in Placentia Bay, Newfoundland (Figure 3.1). The strategy employed was (1) to fit locally-weighted regression models (Cleveland, 1979) to fish weight over the annual cycle for 6 age groups (4-9) monitored from January 1997 to June 2000 and (2) examine the effects of water temperature, feeding, and reproductive state on growth. In fulfilling this goal, a detailed account of the seasonal diet of cod in the study area is provided.

3.3 Material and Methods

Placentia Bay is a large and highly featured embayment, measuring approximately 132 km long by 100 km wide (Figure 3.1). The inner bay is divided by a series of islands into three deep channels that merge to a more open basin in the outer bay.

Biological and oceanographic data were obtained during a series of 24 acoustic surveys conducted between January 1997 and June 2000 (no surveys were conducted in February, March and December), using a calibrated Simrad EK 500 or Biosonics DT 4000 echosounder (Table 3.1). Additional detail of these surveys is given in Mello and Rose (2005). During each survey, water temperature data were obtained using a calibrated Seabird CTD probe. A total of 416 stations covering most depth ranges and regions of the bay were sampled and a mean vertical profile of water temperature and the ambient temperature of cod (i.e., temperature at capture depth, T_A) was calculated for each survey.

Cod were caught from acoustically identified aggregations using a Campelen 1800 bottom trawl or handlines (Table 3.1). Campelen tows were conducted at 3.5 knots for 15 minutes. Handlining was conducted for 30 minutes using four lines each having six equal sized unbaited hooks (10.2 cm long by 2.6 cm wide). For most surveys, fishing sets were conducted in both the inner and outer bay and a total of 5665 fish ages 4-9 were sampled for total length, total weight, somatic weight, gonad weight, sex, and otoliths for age determination. Cod length and weight were measured to the nearest cm and g, respectively. Although fish were captured using two different gears, it was assumed that the selectivity in terms of weight at age was comparable, as neither gear selected by fish girth, as do gillnets.

Stomach contents were analysed from 4239 cod whose stomachs were frozen at sea in plastic bags shortly after extraction. Stomachs that showed signs of regurgitation or damage (e.g., everted) were discarded. In the lab, stomachs were thawed at room temperature, with total contents weighed to the nearest g. Contents were then sorted and identified to species level when possible and classified into 16 prey groups: demersal fishes such as redfish (*Sebastes* sp. L.) and flatfishes (Pleuronectidae), capelin (*Mallotus villosus* Müller), sandlance (*Ammodytes* sp. Reinhardt), other pelagic fishes such as herring (*Clupea harengus* L.), unidentified fishes, echinoderms, molluscs, cnidarians, amphipods, polychaetes, decapods, copepods, malacostracas, other invertebrates (e.g., poriferans), algal material and unidentified prey. Undigested prey was identified using morphological characteristics. Otoliths were used to identify fish in an advanced stage of

digestion. For each cod stomach analysed, the number and the total weight (g) of each prey group was estimated.

For each survey, three indices were used to describe the variability in composition and relative importance of prey items:

1) The relative frequency of occurrence (F_i):

$$F_i = \left(\frac{n_i}{N}\right) * 100 \qquad (1)$$

where for all cod stomachs analysed, n_i is the number of stomachs containing the prey group i and N is the number of non-empty stomachs;

2) The partial fullness index (I_{Pj}):

$$I_{Pj} = \frac{p_j}{l_j^3} * 10^4 \qquad (2)$$

where for each prey group, p_j and l_j are the prey weight (g) and length (cm) of cod j, respectively;

3) The total fullness index (I_{Tj}):

$$I_{Tj} = \sum I_{Pj} \tag{3}$$

For the I_P analysis, invertebrate prey were pooled into two size-groups, as small and large invertebrates (Greenstreet *et al.,* 1998; Nielsen and Andersen, 2001).

A gonado-somatic index (I_{Gj}) was calculated as:

$$I_{Gj} = \left(\frac{d_j}{m_j} \right) \tag{4}$$

where d_j and m_j are the gonad and somatic weight (g) of cod j, respectively.

Loess or locally-weighted regression was used to estimate the average seasonal pattern in somatic weight for cod ages 4-9 that could be tracked during the study period (1990-1993 cohorts). Local regression is a non-parametric technique that returns a predicted value at each point by fitting a weighted linear regression where the weight decreases with distance from the point of interest. Loess regression is robust to the presence of outliers in the data and produce estimates that minimize the variance without distorting underlying patterns in the data (Cleveland and Loader, 1996). Daily estimates of mean somatic weight at age were obtained for the period between 1 January 1997 and 30 June 2000. The model used was:

$$y_k = f(x_k) + \varepsilon_k \quad (5)$$

where y_k is the predicted mean somatic weight at day k, f is the regression function, x_k is the predictor and ε_k is a random error. The span or smoothing factor used in the loess analysis was 0.25 (on a scale of 0 to 1.0). The span consists of the fraction of the data used to estimate the regression surface. Small span values result in fitted curves that follow the data closely, but the curves may be noisy if the span is too small, whereas larger span values increase the smoothness of the fitted curves, but may loose much of the smaller scale variability of the original data as the fit approaches linearity. Because this study is concerned with the short-term (seasonal) variability in somatic weight, a span of 0.25 was considered appropriate. The local parametric function used in the loess regression comprised a model of the Gaussian family and local linear fitting was used as a fitting criterion. Moreover, loess regression often results in predictor variables that are temporally correlated (Ramsey and Schafer, 1997; Battarbee *et al.*, 2002) and as such significance tests were not used nor p-values presented. Instead, the quartile estimation of errors was presented.

The variability in somatic weight of cod j ($r_{j,k}$) was estimated over 30-day periods as follows:

$$r_{j,k} = \frac{(y_{j,k+30} + o_{j,k}) - m_{j,k}}{m_{j,k}} \quad (6)$$

and

$$o_{j,k} = m_{j,k} - y_{j,k} \quad (7)$$

where $m_{j,k}$ is the observed somatic weight of cod j in day k, $y_{j,k+30}$ is the predicted (by Equation 5) mean somatic weight 30 days later and $o_{j,k}$ is the offset, or the difference between the observed and modeled somatic weight on day k. The offset term in the model accounts for the additional variability due to differences in the weight of the cod at the time of sampling relative to the modelled weight. The variability in somatic weight as parameterised in this study is used as a proxy for monthly changes in growth rate. The assumption is that the variability in weight at this temporal scale is due mainly to local conditions (e.g., feeding, temperature) experienced by cod around the time of sampling and hence prevailing over the effect of abiotic and biotic conditions observed at typically larger temporal/spatial scales (e.g., annual growth rate versus latitudinal cline in water temperature).

A general linear model (GLM) was employed to study the seasonal variability in growth for each age group. The predictors initially included T_A, the I_P of all prey groups and I_G. Interactions between predictors (e.g., T_A x I_P) were also investigated. The statistical model used was:

$$Y_i = \beta_0 + \beta_1 X_{i1} + \beta_2 X_{i2} + \ldots + \beta_{p-1} X_{i1} X_{i2} + \varepsilon_i \quad (8)$$

where Y_i is the dependent variable in the i^{th} observation, X_{i1}, X_{i2}, etc., are the values of the predictors in the i^{th} observation, β_0, β_1, β_2,..., β_{p-1} are model parameters, $X_{i1}X_{i2}$ is an interaction term of the main effects X_{i1} and X_{i2}, and ε_i is a random error.

Plots of the normal probability distribution (model residuals x expected normal quartiles) were used to check for the assumption of normal error distribution in all statistical analyses. In all cases, the significance level was set at 5% ($P < 0.05$). The GLM analysis was carried out with SAS statistical software (SAS Institute Inc., 1990), while S-Plus software (MathSoft Inc., 1999) was used for the loess regression. Final models included only those variables found to be statistically significant.

3.4 Results

3.4.1 Temperature

In January the mean water temperature varied little with depth, around 0.3°C during 1998-2000 and 2°C in 1997 (Figure 3.2). A similar profile was observed in April, but the water was colder (0.3°C to 1.3°C) near the surface than in January. By May, surface waters had warmed to 5°C with the onset of thermal stratification and by June the water column was well stratified with a strong thermocline at approximately 50 m. The temperature profile in July was similar, but with warmer surface temperatures (up to 14°C at 10 m). By October and November there was a deepening of the thermocline to about 100 m and the water reached its warmest temperature at depth, ranging from 5-6°C at 50

m. Also of note surface temperatures in the July-October period declined from > 12°C in 1997 to 8-10°C in 1999 and by June 2000 when this study ended, surface the temperature had reached only 6°C.

The mean ambient temperature (T_A) varied seasonally for all ages (ANOVA, $183 \leq n \leq 832$, $P < 0.0001$). However, no significant inter-annual differences in T_A were observed ($P > 0.05$) and the data were pooled across years (1997-2000). Fish were caught in relatively warm water from September to November ($3.2°C \leq T_A \leq 6.0°C$), while from January to July cod were found within a colder water layer ($T_A \leq 1.6°C$) (Table 3.2).

3.4.2 Cod reproductive condition

The mean gonado-somatic index (I_G) varied significantly among months for all age groups (ANOVA, $217 \leq n \leq 974$, $P < 0.002$), but no significant inter-annual differences were observed ($P > 0.05$) and the data were pooled across years (1997-2000). I_G tended to be higher for cod ages 7-9 in all periods (Table 3.3) and peaked in April for age 4 ($I_G = 0.031$) and 9 ($I_G = 0.094$), May for age 5 ($I_G = 0.035$) and June for ages 6-8 ($0.052 \leq I_G \leq 0.090$). Minimum I_G values occurred in January for cod age 4 ($I_G = 0.008$) and in September through October for ages 5-8 ($0.010 \leq I_G \leq 0.018$). Minimum I_G value for age 9 cod occurred in July ($I_G = 0.045$).

3.4.3 Cod diet

A total of 11 phyla, 43 families and 65 prey species were identified in cod stomachs (Appendix 3.1). Empty stomachs occurred more frequently during January (15%), April (12%), July (20%), and through the fall (up to 21% in November) (Table 3.4). Fewer empty stomachs (< 5%) were observed in May, June, August and September.

The stomach content analysis showed that the overall cod diet was highly varied but a few prey comprised most of the contents through the year. The frequency of occurrence (F_i) of decapods (26-80%), amphipods (35-72%) and echinoderms (51% in 1999) was high in cod stomachs in January, as well as in April and May with a combined F_i of 41-64% (Table 3.5). Capelin was present in 24% of cod stomachs in May 2000. By June, decapods ($25\% \leq F_i \leq 80\%$) and amphipods ($63\% \leq F_i \leq 89\%$) were still found in a large portion of cod stomachs, but increasingly capelin ($22\% \leq F_i \leq 59\%$), sandlance ($F_i = 31\%$ in 2000) and demersal fishes ($15\% \leq F_i \leq 20\%$) became frequent prey. Unidentified fishes and capelin ($27\% \leq F_i \leq 40\%$) were still frequent in cod stomachs in July, as were malacostracas ($F_i = 90\%$ in 1998), echinoderms ($F_i = 54\%$ in 1998), amphipods ($F_i = 56\%$ in 1998) and decapods ($F_i = 43\%$ in 1999). Amphipods were present in most cod stomachs in August-September ($70\% \leq F_i \leq 95\%$) but echinoderms, malacostracas and algal material were also frequent ($42\% \leq F_i \leq 63\%$) during this period. The fall diet (October-November) was diverse, but again dominated by amphipods, echinoderms and decapods ($42\% \leq F_i \leq 82\%$). Capelin was present in 33% of stomachs in November 1997, but in the other years capelin was not a frequent diet item during this period. Molluscs,

cnidarians, polychaetes, malacostracas and algal material were also present in cod stomachs through the fall ($11\% \leq F_i \leq 35\%$).

Large invertebrates comprised most of the diet in January ($0.3 < I_P < 0.9$) for most age groups (Figure 3.3). Small invertebrates had high relative contributions to the cod diet particularly in June and September ($1.3 < I_P < 4.8$) for cod ages 4-6 (1997-1998) and ages 7-9 (1998). The diet was more diversified for all ages during the spring in 1999-2000, notably with a higher contribution of large invertebrates. Capelin contribution to the cod diet was relatively high but limited to a few periods of the year, mainly in June ($0.5 < I_P < 2.5$) and to a lesser extent in May and July. The fall diet (October-November) was comprised mainly of invertebrates. The remaining prey groups, including other pelagic and demersal fishes and algal material, typically accounted for a small portion (< 5%) of the overall diet in all seasons. The total fullness index (I_T) varied between 0.1 and 5.3, reaching minimum values in April or November and peaking in June for all age groups, except for age 6 cod in 1997 (September) and age 8 in 2000 (May). I_T was two to four folds higher in June and September 1998 when compared with the other years, particularly for younger cod (ages 4-6).

3.4.4 Cod growth

A total of 3838 fish ages 4-9 were used in the loess regression analysis of the seasonal pattern in somatic weight. Fish were pooled by year of birth, which allowed both inter-seasonal and inter-annual variability of the data to be included in the model. The model

explained between 33-55% of the observed variance in the data (Table 3.6). Model residuals were small. The quartile estimation show that most residuals varied from –0.49 to 0.38 (1^{st} and 3^{rd} quartiles, respectively) and the median was close to zero ($-0.09 \leq$ median ≤ -0.04) indicating that no apparent departures from normality were detected.

Box plots of the somatic weight data (raw data) and the mean predicted by the loess model showed a distribution with recognisable seasonal cycles, but more pronounced for the older fish of the different cohorts (Figure 3.4). The model fit appeared to be satisfactory as the predicted weight followed the raw data closely, overlapping in most cases the median estimates through the time series. The somatic weight of cod of the 1993 cohort (age 4 in 1997) varied mostly between 0.4-1.2 kg (1^{st} and 3^{rd} quartiles). The 1992 cohort (age 5 in 1997) ranged between 0.8-1.7 kg and the 1991 cohort (age 6 in 1997) between 0.9-2.2 kg. The 1990 cohort (age 7 in 1997) weighed between 1.2-3.0 kg. Earlier cohorts could not be analyzed over the seasons, but for age 8 and 9 somatic weight varied mostly between 1.5-3.5 kg, and 1.6-4.0 kg. In most cases, the somatic weight declined through the winter, reached minimum values at the beginning of the spring (April-May) and then increased through the summer and peaked in the fall (November). The maximum inter-seasonal variability in somatic weight was observed for the youngest cod in all years (1993 cohort), reaching 70% in 1997, but then decreased at an annual rate of approximately 10% until June 2000 (Figure 3.5). Similar trends were observed for the remaining cohorts (except for the 1990 cohort in 1998), but somatic weight varied mostly between 18% and 40% in all years.

Data from 2659 fish for which all measurements were available (June 1998 to November 1999) were used in a regression analysis of the effect of ambient temperature (T_A), feeding (I_P) and the development of reproductive tissues (I_G) on cod growth rate over 30-day intervals (*r*). The fitted model was highly significant for all age groups ($P < 0.0001$) and explained between 31-52% of the data variance (Table 3.7). Temperature had a significant effect on growth for all ages and accounted for most of the explained variance for ages 6-8. The effect of temperature on growth was positive for ages 4-7, but negative for ages 8-9 as indicated by the regression coefficients (c). The partial fullness index (I_P) of several prey groups also had significant effects on growth. The I_P of capelin had a significant effect on growth of all age groups, except age 8 and explained most of the variance for ages 4-5. The I_P of small invertebrates had a significant effect on growth of ages 4, 5, 8 and 9, while the I_P of large invertebrates (ages 4-7), sandlance (age 6) and demersal fishes (age 9) had age specific effects in the model. The interaction term between temperature and I_P of small invertebrates was significant for cod age 6. The I_P of capelin, sandlance, demersal fishes, large invertebrates and the interaction terms had positive effects on growth. In addition, the gonado-somatic index (I_G) had a significant negative effect for age 7 cod.

In most cases the growth rate predicted by the model peaked in June ($0.05 < r < 0.14$ for ages 4-5 and $0.03 < r < 0.05$ for older cod), except for cod age 5 (in 1998), 8 and 9 (in 1999) when growth peaked in November (Figure 3.6). Growth rates declined in July ($r <$ 0.11 for ages 4-5 and < 0.04 for older cod) and reached minimum values ($-0.04 < r <$ 0.03) in October or November (ages 4-7) and January (ages 8-9). The growth rate

increased between October-November for cod ages 5, 7, and 8. The residuals were scattered around zero, indicating that no major departure from normality could be detected, and that model assumptions were not violated.

3.5 Discussion

The growth of Placentia Bay cod showed marked seasonal and age-specific variability. Younger cod (ages 4-5) exhibited the largest seasonal differences in somatic weight (up to 70% between spring-fall). Water temperature and diet (particularly capelin) accounted for most of the explained variance in growth for all ages. However, the data indicate that the development of reproductive tissues also had a significant effect on growth (age 7). The relationship between predator and prey size is evident in these data. For example, large invertebrates were related to growth rate of cod ages 4-7, but for age 9 cod, demersal fishes were important in accounting for growth variation. The effect of temperature and feeding on growth and size dependency between prey and cod in Placentia Bay are consistent with findings observed for other cod stocks in the North Atlantic (Hop *et al.*, 1992; Brander, 1995; Bogstad and Mehl, 1997).

The regression analysis showed that temperature had both significant positive (ages 4-7) and negative (ages 8-9) effects on growth. Cod of all ages experienced a rapid increase in somatic weight in June-July when cod were found in colder waters ($< 2^{\circ}C$), food intake was maximum (total fullness index peaked in June in most cases), but feeding activity was variable ($1\% \leq$ empty stomachs $\leq 20\%$) suggesting that prey availability (particularly

capelin) differed among areas of the bay where cod were found. With the onset of the fall, the growth rate decreased for all ages (except for ages 8-9 in 1999) and was smallest by October or November when somatic weight peaked and the ambient temperature was warmest, but feeding was minimal (total fullness index < 0.05). These findings suggest that when food is not a limiting factor, growth tends to increase even when fish occupy colder waters, but when food is limiting, the opposite may occur. Such results underscore the role of changing metabolic costs in relation to temperature, feeding conditions and growth (Jobling, 1982; Michalsen *et al.*, 1998; Pálsson and Thorsteinsson 2003).

The negative effect of temperature on growth (ages 8-9) could be explained by age differences in distribution. Mello and Rose (2005) estimated that cod density indices increased from April to July 1999 in both inner bay and outer bay (from 0.003 to 0.015 fish.m^{-2} and from 0.001 to 0.003 fish.m^{-2}, respectively) and from October to November, particularly in the inner bay (from 0.001 to 0.004 fish.m^{-2}). Such findings are related to the seasonal movement of cod from adjacent stocks in and out of the bay and mixing with Placentia Bay cod (Davis *et al.* 1994; Lawson and Rose 2000). Changes in feeding opportunities and habitat usage during these periods might lead to density-dependent shifts in the distribution of older cod. Swain (1993) suggested that density-dependent shifts in the distribution of cod entail a trade-off between density dependent benefits of greater food supply in shallow/warmer water and lower metabolic costs (and growth) for older fish inhabiting colder water. Similar effects have been identified for Icelandic cod (Pálsson and Thorsteinsson, 2003). Although, the data used in the present study do not

allow an analysis of density-dependent bathymetric patterns, the negative effect of temperature on growth rates of older cod are consistent with this hypothesis

Overall, amphipods, decapods and echinoderms dominated the cod diet in most periods, but capelin (mainly), sandlance and demersal fishes were important during June-July. Amphipods were particularly common in cod stomachs in June for all ages ($63\% \leq F_i \leq 89\%$) when capelin was available. Amphipods are a common prey of capelin (Gerasimova, 1994) and these are possibly also fed upon by cod while pursuing capelin. These findings differ somewhat from seasonal diet findings for other cod stocks. For example, Turuk (1968) reported that cod from southern Labrador fed largely on capelin during the fall-winter, while cod from the eastern Newfoundland Shelf and northeast Grand Bank fed on capelin during the winter and through the year, respectively. Similar findings were reported by Lilly (1991) regarding the fall diet of cod from southern Labrador. Schwalme and Chouinard (1999) found that fish, mainly Atlantic herring, was the most important prey of large cod from the southern Gulf of St. Lawrence in all seasons, except winter, while Hop *et al.* (1992) showed that small and lager cod from southern Norway, fed mainly on large invertebrates and fish during the winter and on large invertebrates for most sizes cod during summer and fall. Such comparisons confirm that cod-prey relationships are stock-specific (Hanson and Chouinard, 2002), with cod being typically an opportunistic predator (Klemetsen, 1982; Hop *et al.*, 1993).

The development of reproductive tissues had a significant negative effect on growth of age 7 cod. The effect may be related to the large production of eggs by older cod (Powles

1958; May 1967) and the allocation of most energy reserves to the growth of reproductive tissues and reduction of somatic growth (Chen and Mello, 1999).

This study shows that somatic weight peaks in the fall for all ages when fish are found in the warmest waters, but food intake is low and dominated by invertebrates. A possible explanation relates to the effect of summer feeding migrations undertaken by larger cod. Larger cod from Placentia Bay tend to disperse out of the bay during the summer and return during the fall (Lawson and Rose, 2000). In addition, experiments done with Icelandic cod reared in laboratory and subjected to unlimited feeding showed that growth rates increased with temperature until an optimal threshold was reached and then decreased with any further increase in temperature (Björnsson *et al.*, 2001), while another study showed that temperature had a relatively greater effect on the growth rate of smaller rather than larger cod (Björnsson and Steinarsson, 2002). Hence, it is possible that Placentia Bay cod exhibit two strategies with respect to growth. Larger migratory cod may enrich their diet and enhance growth (as observed in the fall 1999 for ages 8-9) by carrying out feeding migrations, a behaviour common to several North Atlantic cod stocks (Rose, 1993; Brander, 1994; Pálsson and Thorsteinsson, 2003), whereas smaller non-migratory cod may enhance growth by inhabiting warmer waters.

A key finding of this study relates to the role of capelin in the increase in somatic weight of cod during June-July. It appears that the high lipid content (Jangaard, 1974; Montevecchi and Piatt, 1984) and availability of capelin at this time of the year allowed cod to increase weight rapidly despite colder water temperatures and moderate to high

gonado-somatic activity. Previous studies have investigated the importance of capelin to cod growth on an annual scale (Krohn *et al.*, 1997; Vilhjálmsson, 2002), but this is the first study that identifies the time of the year (at least for this stock) when feeding by cod on capelin strongly influences growth in somatic weight.

Given the apparent importance of capelin to cod, it would be expected that the lack of such lipid rich prey might be a factor affecting the recovery of several depleted cod stocks (Rose and O'Driscoll, 2002). For example, Vilhjálmsson (2002) reported that the average weight of Icelandic cod (ages 5-8) decreased by 25-30% in the early 1980s and 1990s when capelin stocks were low and cod of intermediate age or size were unable to find replacement food. Similar findings were reported for cod in the Barents Sea (Jørgensen, 1992; Ozhigin *et al.*, 1994). In addition, the decrease in capelin consumption by cod has been related to the reduction in fecundity of mature Arctic-Norwegian cod (Kjesbu *et al.*, 1998) and increased mortality of spawning females in northern Gulf of St. Lawrence (Lambert and Dutil, 2000).

While the absolute status of capelin stocks is uncertain, acoustic survey estimates indicate a sudden decline in capelin abundance off the northeast Newfoundland and Labrador in the early 1990s that has persisted through the present day (DFO, 2002). This decline was accompanied by a southerly shift in capelin distribution (Carscadden and Nakashima, 1997; Mowbray, 2002) and by major changes in capelin spawning biology, including delays in spawning time from four to six weeks and reduced spawner size (Nakashima, 1996; Carscadden and Nakashima, 1997; Carscadden *et al.* 1997). In the case of Placentia

Bay cod, delayed capelin spawning in coastal areas, reduced sizes, or declines in abundance would likely cause a reduction in availability of this prey item during the time of the year when the results of this study indicate they are most important to cod.

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3.7 References

Battarbee, R.W., Grytnes, J.-A., Thompson, R., Appleby, P.G., Catalan, J., Korhola, A., Birks, H.J.B., Heegaard, E., and Lami, A. 2002. Comparing paleolimnological and instrumental evidence of climate change for remote mountain lakes over the last 200 years. Journal of Paleolimnology, 28: 161-179.

Bergstedt, R.A., and Swink, W.D. 1995. Seasonal growth and duration of the parasitic life stage of the landlocked sea lamprey (*Petromyzon marinus*). Canadian Journal of Fisheries and Aquatic Sciences, 52: 1257-1264.

Björnsson, B. and Steinarsson, A. 2002. The food-unlimited growth rate of Atlantic cod (*Gadus morhua*). Canadian Journal of Fisheries and Aquatic Sciences, 59: 494-502.

Björnsson, B., Steinarsson, A., and Oddgeirsson, M. 2001. Optimal temperature for growth and feed conversion of immature cod (*Gadus morhua* L.). ICES Journal of Marine Science, 58: 29-38.

Bogstad, B., and Mehl, S. 1997. Interactions between Atlantic cod (*Gadus morhua*) and its prey species in the Barents Sea. *In*: Proceedings of the international symposium on the role of forage fishes in marine ecosystems. Lowell Wakefield Fisheries Symposium Series, 14: 591-615.

Brander, K.M. 1995. The effect of temperature on growth of Atlantic cod (*Gadus morhua* L.). ICES Journal of Marine Science, 52: 1-10.

Brander, K.M. 1994. Spawning and life history information for North Atlantic cod stocks. ICES Cooperative Research Report No. 205.

Carscadden, J.E., and Nakashima, B.S. 1997. Abundance and changes in distribution, biology and behaviour of capelin in response to cooler waters of the 1990s. *In*: Proceedings of the international symposium on the role of forage fishes in marine ecosystems. Lowell Wakefield Fisheries Symposium Series, 14: 457-468.

Carscadden, J.E., Nakashima, B.S., and Frank, K.T. 1997. Effects of fish length and temperature on the timing of peak spawning in capelin *(Mallotus villosus)*. Canadian Journal of Fisheries and Aquatic Sciences, 54: 781-787.

Chen, Y., and Mello, L.G.S. 1999. Growth and maturation of cod (*Gadus morhua*) of different year classes in the Northwest Atlantic, NAFO subdivision 3Ps. Fisheries Research, 42: 87-101.

Chiu, T.S. and Chen, C.S. 2001. Growth and temporal variation in Japanese anchovy cohorts during their recruitment to the East China Sea. Fisheries Research, 53: 1-15.

Cleveland, W.S. 1979. Robust locally-weighted regression and smoothing scatter plots. Journal of the American Statistical Association, 74: 829-836.

Cleveland, W.S., and Loader, C. 1996. Smoothing by local regression: principles and methods. Statistical theory an computational aspects of smoothing. *In*: Proceedings of the COMPSTAT '94 Satellite Meeting 10-49.

Coggan, R. 1997. Seasonal and annual growth rates in the Antarctic fish *Notothenia coriiceps* Richardson. Journal of Experimental Marine Biology and Ecology, 213: 215-229.

Cubillos, L.A., Arcos, D.F., Bucarey, D.A., and Canales, M.T. 2001. Seasonal growth of small pelagic fish off Talcahuano, Chile (37 degree S, 73 degree W): A consequence of their reproductive strategy to seasonal upwelling? Aquatic Living Resources, 14: 115-124.

Daan, N. 1974. Growth of north seas cod, *Gadus morhua*. Netherlands Journal of Sea Research, 8: 27-48.

Davis, M. B., Lundrigan, P., and Ripley, R. 1994. A description of cod stock structure in Placentia Bay, NAFO Subdivision 3Ps. DFO Atlantic Fisheries Research Document 94/32.

DFO 2001. Capelin in Subarea 2+Div.3KL. Update. DFO Science Stock Report B2-02 (2001). Ottawa.

Essington, T.E., Kitchell, J.F., and Walters, C.J. 2001. The von Bertalanffy growth function, bioenergetics, and the consumption rates of fish. Canadian Journal of Fisheries and Aquatic Sciences, 58: 2129-2138.

Fabré, N.N., and St. Paul, U. 1998. Annulus formation on scales and seasonal growth of the central amazonian anostomid *Schizodon fasciatus*. Journal of Fish Biology, 53: 1-11.

Fontoura, N.F., and Agostinho, A.A. 1996. Growth with seasonally varying temperatures: an expansion of the von Bertalanffy growth model. Journal of Fish Biology, 48: 569-584.

Francis, M.P., Mulligan, K.P., Davies, N.M., and Beentjes, M.P. 1999. Age and growth estimates for New Zealand hapuku, *Polyprion oxygeneios*. Fishery Bulletin, 97: 227-242.

Gauldie, R.W. 1990. How often is the von Bertalanffy-type length-at-age curve in fishes related to weight change artefacts interpreted as age rings in otoliths? Comparative Biochemistry and Physiology, 96A: 451-458.

Gerasimova, O. V. 1994. Peculiarities of spring feeding by capelin (*Mallotus villosus*) on the Grand Bank in 1987-90. Journal of Northwest Atlantic Fisheries Science, 17: 59-67.

Greenstreet, S.P.R., McMillan J.A., and Armstrong, E. 1998. Seasonal variation in the importance of pelagic fish in the diet of piscivorous fish in the Moray Firth, NE Scotland: a response to variation in prey abundance? ICES Journal of Marine Science, 55: 121-133.

Hanson, J.M., and Chouinard, G.A. 2002. Diet of Atlantic cod in southern Gulf of St. Lawrence as an index of ecosystem change, 1959-2000. Journal of Fish Biology, 60: 902-922.

Hop, H., Gjøsæter, J., and Danielssen, D.S. 1992. Seasonal feeding ecology of cod (*Gadus morhua* L.) on the Norwegian Skagerrak coast. ICES Journal of Marine Science, 49: 453-461.

Hop, H., Danielssen, D.S., and Gjøsæter, J. 1993. Winter feeding ecology of cod (*Gadus morhua*) in a fjord of southern Norway. Journal of Fish Biology, 43: 1-18.

Ipatov, V.V., and Uzars, D.V. 1981. Food supply as a factor in seasonal changes in metabolism of Baltic cod. Canadian Translation of Fisheries and Aquatic Sciences 5453.

Jangaard, P.M. 1974. The capelin (*Mallotus villosus*). Biology, distribution, exploitation, utilization, and composition. Bulletin of the Fisheries Research Board of Canada 186.

Jørgensen, T. 1992. Long-term changes in growth of North-east Arctic cod (*Gadus morhua*) and some environmental influences. ICES Journal of Marine Science, 49: 263-277.

Jobling, M. 1982. Food and growth relationships of the cod, *Gadus morhua* L., with special reference to Balsfjorden, north Norway. Journal of Fish Biology, 21: 357-371.

Kjesbu, O.S., Witthames, P.R., Solemdal, P., and Walker, M.G. 1998. Temporal variations in the fecundity of Arcto-Norwegian cod (*Gadus morhua*) in response to natural changes in food and temperature. Journal of Sea Research, 40: 303-321.

Klemetsen, A. 1982. Food and feeding habits of cod from the Balsfjord, northern Norway during a one-year period. ICES Journal of Marine Science, 40: 101-111.

Krohn, M., Reidy, S., and Kerr, S. 1997. Bioenergetic analysis of the effects of temperature and prey availability on growth and condition of northern cod (*Gadus morhua*). Canadian Journal of Fisheries and Aquatic Sciences, 54: 113-121.

Lambert, Y., and Dutil, J.-D. 2000. Energetic consequences of reproduction in Atlantic cod (*Gadus morhua*) in relation to spawning level of somatic energy reserves. Canadian Journal of Fisheries and Aquatic Sciences, 57: 815-825.

Lawson, G.L., and Rose, G.A. 2000. Seasonal distribution and movements of coastal cod (*Gadus morhua*) in Placentia Bay, Newfoundland. Fisheries Research, 49: 61-75.

Lilly, G.R. 1991. Interannual variability in predation by cod (*Gadus morhua*) on capelin (*Mallotus villosus*) and other prey off southern Labrador and northeastern Newfoundland. ICES Marine Science Symposium, 193: 133-146.

MathSoft 1999. S-plus 2000. Programmer's guide. MathSoft, Inc., Seattle, Washington.

May, A.W. 1967. Fecundity of Atlantic cod. Journal of the Fisheries Research Board of Canada, 24: 1531-1551.

McGarvey, R., and Fowler, A.J. 2002. Seasonal growth of King George whiting (*Sillaginodes punctata*) estimated from length-at-age samples of the legal-size harvest. Fishery Bulletin, 100: 545-558.

Mello, L.G.S., and Rose, G.A. 2005. Using geostatistics to quantify seasonal distribution and aggregation patterns of fishes: an example of Atlantic cod (*Gadus morhua*). Canadian Journal of Fisheries and Aquatic Sciences, 62: 659-670.

Michalsen, K., Ottersen, G., and Nakken, O. 1998. Growth of North-east Arctic cod (*Gadus morhua* L.) in relation to ambient temperature. ICES Journal of Marine Science, 55: 863-877.

Montevecchi, W.A., and Piatt, J.F. 1984. Composition and energy contents of mature inshore spawning capelin (*Mallotus villosus*): implications for seabird predators. Comparative Biochemistry and Physiology, 78A: 15-20.

Mowbray, F.K. 2002. Changes in the vertical distribution of capelin (*Mallotus villosus*) off Newfoundland. ICES Journal of Marine Science, 59: 942-949.

Mulligan, T.J., and Leaman, B.M. 1992. Length-at-age analysis: Can you get what you see? Canadian Journal of Fisheries and Aquatic Sciences, 49: 632-643.

Nakashima, B.S. 1996. The relationship between oceanographic conditions in the 1990s and changes in spawning behaviour, growth and early life history of capelin (*Mallotus villosus*). NAFO Scientific Council Studies, 24: 55–68.

Nielsen, J.R., and Andersen, M. 2001. Feeding habits and density patterns of Greenland cod, *Gadus ogac* (Richardson 1836), at West Greenland compared to those of the coexisting Atlantic cod, *Gadus morhua* L. Journal of Northwest Atlantic Fishery Science, 29: 1-22.

Nilssen, E.M., Pedersen, T., Hopkins, C.C.E., Thyholt, K., and Pope, J.G. 1994. Recruitment variability and growth of Northeast Arctic cod: Influence of physical environment, demography, and predator-prey energetics. ICES Marine Science Symposium, 198: 449-470.

Ozhigin, V.K., Tretyak, V.L., Yaragina, N.A., and Ivshin, V.A. 1994. Dependence of the Barents Sea cod growth upon conditions of their feeding on capelin and water temperature. ICES Council Meeting Papers 1994/G:32.

Pálsson, Ó. K., and Thorsteinsson, V. 2003. Migration patterns, ambient temperature, and growth of Icelandic cod (*Gadus morhua*): evidence from storage tag data. Canadian Journal of Fisheries and Aquatic Sciences, 60: 1409-1423.

Powles, P.M. 1958. Studies of reproduction and feeding of Atlantic cod (*Gadus callarias* L.) in the southwestern Gulf of St. Lawrence. Journal of the Fisheries Research Board of Canada, 15: 1383-1402.

Ramsey, F.L., and Schafer, D.W. 1997. The statistical sleuth. A course in methods of data analysis. Duxbury Press, London.

Rose, G.A. 1993. Cod spawning on a migration highway in the North-west Atlantic. Nature, 366: 458-461.

Rose, G. A., and Leggett, W. C. 1990. The importance of scale to predator-prey spatial correlations: An example of Atlantic fishes. Ecology, 71: 33-43.

Rose, G.A., and O'Driscoll, R.L. 2002. Capelin are good for cod: can the northern stock rebuild without them? ICES Journal of Marine Science, 59: 1018-1026.

SAS 1990. SAS/STAT User's guide, Volume 1. SAS Institute Inc., Cary, NC.

Schwalme, K., and Chouinard, G.A. 1999. Seasonal dynamics in feeding, organ weights, and reproductive maturation of Atlantic cod (*Gadus morhua*) in the southern Gulf of St. Lawrence. ICES Journal of Marine Science, 56: 303-319.

Shulman, G.E. 1974. Life cycles of fish: physiology and biochemistry. John Wiley and Sons, New York.

Swain, D.P. 1993. Age- and density-dependent bathymetric pattern of Atlantic cod (*Gadus morhua*) in the southern Gulf of St. Lawrence. Canadian Journal of Fisheries and Aquatic Sciences, 50: 1255-1264.

Turuk, T.N. 1968. Seasonal changes of cod feeding in the Labrador and Newfoundland areas in 1964-1966. TRUDY PINRO, 23: 370-382.

Vilhjálmsson, H. 2002. Capelin (*Mallotus villosus*) in the Iceland-East Greenland-Jan Mayen ecosystem. ICES Journal of Marine Science, 59: 870-883.

3.8 Tables

Table 3.1 Number of cod ages 4-9 sampled, gear type and the number of fishing sets per stratum during acoustic surveys in Placentia Bay. T = bottom trawl, and L = handline.

Date		No. fish	Gear	No. fishing sets	
Year	Date	sampled		Inner bay	Outer bay
1997	14-16 Jan	206	T	2	1
	6-12 Apr	178	L	3	2
	21-30 Jun	270	L	3	10
	6-12 Aug	160	L	9	7
	27-29 Sep	74	L	5	4
	4-22 Nov	191	L	10	6
1998	6-8 Jan	482	T	4	2
	14-19 Apr	191	L	0	3
	11-28 May	82	L	3	2
	19-22 Jun	557	T	2	5
	1-5 Jul	234	L	2	0
	10-14 Sep	24	L	1	0
	22-30 Oct	170	L	8	3
	2-27 Nov	350	L	26	4
1999	14-15 Jan	166	T	3	1
	7-22 Apr	373	L	7	5
	4-22 May	117	L	6	3
	2-5 Jun	682	T	3	5
	15-27 Jul	220	L	6	9
	22-30 Oct	134	L	2	1
	2-30 Nov	246	L	10	5
2000	4-7 Apr	100	L	2	1
	5-14 May	106	L	8	7
	6-9 Jun	352	T	2	5
	Total	5,665		127	91

Table 3.2 Mean (SD) of ambient temperature (T_A) of cod ages 4-9 caught during surveys in Placentia Bay (1997–2000). The data are pooled across years.

Month	Age 4	5	6	7	8	9
			°C			
Jan	0.1 (0.3)	0.1 (0.3)	0.2 (0.1)	0.3 (0.1)	0.2 (0.5)	0.5 (0.6)
Feb	-	-	-	-	-	-
Mar	-	-	-	-	-	-
Apr	0.3 (0.1)	0.3 (0.1)	0.3 (0.1)	0.4 (0.1)	0.4 (0.1)	0.3 (0.1)
May	0.1 (0.4)	0.2 (0.4)	0.1 (0.4)	0.1 (0.4)	0.1 (0.4)	-0.1 (0.3)
Jun	1.1 (0.5)	0.9 (0.4)	1.1 (0.4)	1.1 (0.2)	1.0 (0.4)	1.1 (0.3)
Jul	1.6 (0.3)	1.5 (0.3)	1.5 (0.3)	1.4 (0.2)	1.4 (0.3)	1.6 (0.3)
Aug	-	-	-	-	-	-
Sep	6.0 (0.1)	6.0 (0.1)	6.0 (0.1)	6.0 (0.1)	6.0 (0.1)	-
Oct	4.2 (1.5)	5.4 (1.4)	4.6 (1.8)	4.9 (0.1)	4.9 (0.1)	-
Nov	3.2 (1.4)	3.4 (1.5)	3.6 (1.7)	3.7 (1.5)	3.3 (1.9)	3.5 (1.1)
Dec	-	-	-	-	-	-

Table 3.3 Mean (SD) of the gonado-somatic index (I_G) of cod ages 4-9 sampled in Placentia Bay (1997–2000). The data are pooled across years. n = number of fish.

Month	n	Age					
		4	5	6	7	8	9
Jan	555	0.008 (0.001)	0.017 (0.002)	0.031 (0.003)	0.039 (0.003)	0.067 (0.042)	0.056 (0.053)
Feb		-	-	-	-	-	-
Mar		-	-	-	-	-	-
Apr	345	0.031 (0.020)	0.028 (0.030)	0.047 (0.036)	0.059 (0.039)	0.077 (0.053)	0.094 (0.052)
May	211	0.019 (0.009)	0.035 (0.003)	0.036 (0.003)	0.063 (0.004)	0.069 (0.004)	0.064 (0.003)
Jun	965	0.013 (0.021)	0.027 (0.030)	0.052 (0.050)	0.077 (0.052)	0.090 (0.061)	0.089 (0.058)
Jul	280	0.012 (0.003)	0.011 (0.007)	0.037 (0.005)	0.038 (0.005)	0.050 (0.007)	0.045 (0.010)
Aug		-	-	-	-	-	-
Sep	27	0.013 (0.010)	0.015 (0.004)	0.022 (0.002)	0.018 (0.002)	0.011 (0.005)	-
Oct	54	0.015 (0.006)	0.010 (0.006)	0.013 (0.006)	0.038 (0.004)	0.014 (0.001)	-
Nov	967	0.022 (0.002)	0.022 (0.002)	0.023 (0.002)	0.029 (0.003)	0.033 (0.003)	0.056 (0.005)
Dec		-	-	-	-	-	-
Total	3,404						

Table 3.4 Total number and percentage of empty cod stomachs sampled per month in Placentia Bay (1997-2000). The data are pooled across years.

Month	Stomach	
	Number	% Empty
Jan	664	15
Feb	-	-
Mar	-	-
Apr	367	12
May	234	4
Jun	1184	< 1
Jul	292	20
Aug	130	< 1
Sep	75	< 1
Oct	105	14
Nov	1188	21
Dec	-	-
Total	4239	

Table 3.5 Frequency of occurrence (F_i) of different prey groups found in stomachs of Placentia Bay cod. F_i is the percentage of stomachs containing prey group i of non-empty stomachs.

Year	Prey group	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1997	Demersal fishes	-	-	-	-	-	-	-	-	-	-	-	-
	Capelin	-	-	-	-	-	50	-	-	-	-	33	-
	Sandlance	-	-	-	-	-	-	-	-	-	-	-	-
	Pelagic fishes	-	-	-	-	-	-	-	-	-	-	-	-
	Unindentified fishes	-	-	-	-	-	38	-	34	19	17	10	-
	Echinoderms	-	-	-	-	-	50	-	22	61	17	40	-
	Molluscs	-	-	-	-	-	50	-	4	13	-	15	-
	Cnidarians	-	-	-	-	-	-	-	6	-	-	15	-
	Amphipods	-	-	-	-	-	67	-	83	70	75	52	-
	Polychaetes	-	-	-	-	-	-	-	-	-	-	8	-
	Decapods	-	-	-	-	-	25	-	31	42	33	16	-
	Copepods	-	-	-	-	-	-	-	-	-	-	-	-
	Malacostracas	-	-	-	-	-	39	-	28	42	17	18	-
	Other invertebrates	-	-	-	-	-	-	-	6	50	-	-	-
	Algal material	-	-	-	-	-	-	-	23	47	17	17	-
	Unindentified material	-	-	-	-	-	7	-	28	34	39	45	-
1998	Demersal fishes	22	-	-	-	-	7	-	-	33	-	8	-
	Capelin	4	-	-	-	-	59	-	-	18	-	6	-
	Sandlance	1	-	-	-	-	4	-	-	-	-	1	-
	Pelagic fishes	-	-	-	-	-	2	-	-	-	-	2	-
	Unindentified fishes	27	-	-	-	-	25	29	-	19	23	20	-
	Echinoderms	5	-	-	-	-	4	54	-	25	39	42	-
	Molluscs	34	-	-	-	-	4	-	-	-	25	3	-
	Cnidarians	1	-	-	-	-	5	-	-	-	12	5	-
	Amphipods	72	-	-	-	-	89	56	-	95	48	35	-
	Polychaetes	13	-	-	-	-	5	32	-	-	25	5	-
	Decapods	79	-	-	-	-	32	26	-	27	42	29	-
	Copepods	-	-	-	-	-	-	-	-	-	-	-	-
	Malacostracas	32	-	-	-	-	7	90	-	63	24	17	-
	Other invertebrates	1	-	-	-	-	5	-	-	-	-	1	-
	Algal material	5	-	-	-	-	7	4	-	6	35	22	-
	Unindentified material	39	-	-	-	-	8	9	-	-	26	21	-

Table 3.5 (cont.). Frequency of occurrence (F_i) of different prey groups found in stomachs of Placentia Bay cod. F_i is the percentage of stomachs containing prey group i of non-empty stomachs.

Year	Prey group	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1999	Demersal fishes	-	-	-	3	3	15	3	-	-	18	19	3
	Capelin	14	-	-	1	4	49	27	-	-	-	2	-
	Sandlance	-	-	-	-	-	7	9	-	-	-	9	-
	Pelagic fishes	-	-	-	2	11	11	-	-	-	-	25	3
	Unindentified fishes	24	-	-	9	18	22	40	-	-	18	16	5
	Echinoderms	51	-	-	58	62	11	19	-	-	82	65	76
	Molluscs	-	-	-	3	9	1	4	-	-	23	8	4
	Cnidarians	-	-	-	3	6	3	2	-	-	14	5	14
	Amphipods	35	-	-	35	26	76	21	-	-	63	30	47
	Polychaetes	9	-	-	12	11	15	8	-	-	20	16	14
	Decapods	26	-	-	40	42	80	43	-	-	49	45	34
	Copepods	17	-	-	-	-	1	-	-	-	-	-	-
	Malacostracas	15	-	-	5	6	23	18	-	-	-	22	12
	Other invertebrates	4	-	-	5	6	6	3	-	-	-	13	4
	Algal material	28	-	-	20	38	8	22	-	-	49	47	63
	Unindentified material	21	-	-	26	20	7	16	-	-	27	25	20
2000	Demersal fishes	-	-	-	-	7	20	-	-	-	-	-	-
	Capelin	-	-	-	-	24	22	-	-	-	-	-	-
	Sandlance	-	-	-	-	-	31	-	-	-	-	-	-
	Pelagic fishes	-	-	-	-	-	-	-	-	-	-	-	-
	Unindentified fishes	-	-	-	-	33	25	-	-	-	-	-	-
	Echinoderms	-	-	-	-	54	7	-	-	-	-	-	-
	Molluscs	-	-	-	-	8	4	-	-	-	-	-	-
	Cnidarians	-	-	-	-	9	5	-	-	-	-	-	-
	Amphipods	-	-	-	-	63	63	-	-	-	-	-	-
	Polychaetes	-	-	-	-	8	18	-	-	-	-	-	-
	Decapods	-	-	-	-	36	77	-	-	-	-	-	-
	Copepods	-	-	-	-	-	-	-	-	-	-	-	-
	Malacostracas	-	-	-	-	52	44	-	-	-	-	-	-
	Other invertebrates	-	-	-	-	-	4	-	-	-	-	-	-
	Algal material	-	-	-	-	35	9	-	-	-	-	-	-
	Unindentified material	-	-	-	-	35	10	-	-	-	-	-	-

Table 3.6 Results of the loess regression analysis of seasonal patterns in somatic weight of cod ages 4-9 (1990-1993 cohorts). n = number of fish, r^2 = regression coefficient, 1^{st} Q = first quartile and 3^{rd} Q = third quartile.

Cohort	n	r^2	Residuals					
			SD	Min.	1^{st} Q	Median	3^{rd} Q	Max.
1990	568	0.33	0.7	-1.53	-0.49	-0.09	0.38	2.1
1991	497	0.42	0.52	-1.24	-0.31	-0.06	0.23	1.82
1992	1,649	0.47	0.41	-1.01	-0.28	-0.05	0.2	1.65
1993	1,124	0.55	0.35	-0.96	-0.24	-0.04	0.18	1.53
Total	3,838							

Table 3.7 Results of a regression analysis of ambient temperature (T_A), partial fullness index (I_P) and gonado-somatic index (I_G) on cod growth over 30-day intervals. Only significant effects are presented ($P < 0.05$). c = coefficient of the regression function for each age group, df = degrees of freedom and r^2 = regression coefficient. Superscript $^+$ = intercept.

Age	Source	r^2	df	F	P > F	c (SD)
4	Model	0.41	401	28.5	< 0.0001	0.091 (0.006)$^+$
	T_A		1	12.8	0.0004	0.051 (0.014)
	I_P capelin		1	51.3	< 0.0001	0.041 (0.005)
	I_P small invertebrates		1	18.4	< 0.0001	-0.018 (0.005)
	I_P large invertebrates		1	23.6	< 0.0001	0.047 (0.009)
5	Model	0.31	693	24.7	< 0.0001	0.073 (0.005)$^+$
	T_A		1	15.7	< 0.0001	0.048 (0.012)
	I_P capelin		1	50.8	< 0.0001	0.048 (0.006)
	I_P small invertebrates		1	28.9	< 0.0001	-0.019 (0.004)
	I_P large invertebrates		1	10.3	0.001	0.029 (0.009)
6	Model	0.40	705	45	< 0.0001	0.034 (0.002)$^+$
	T_A		1	54.5	< 0.0001	0.041 (0.005)
	I_P capelin		1	41.5	< 0.0001	0.013 (0.002)
	I_P large invertebrates		1	5.7	0.01	0.007 (0.003)
	I_P sandlance		1	3.3	0.05	0.016 (0.008)
	T_A x I_P small invertebrates		1	23.5	< 0.0001	0.025 (0.005)

Table 3.7 (cont.) Results of a regression analysis of ambient temperature (T_A), partial fullness index (I_P) and gonado-somatic index (I_G) on cod growth over 30-day intervals. Only significant effects are presented ($P < 0.05$). c = coefficient of the regression function for each age group, df = degrees of freedom and r^2 = regression coefficient. Superscript $^+$ = intercept

Age	Source	r^2	df	F	P > F	c (SD)
7	Model	0.41	493	38.8	< 0.0001	0.024 (0.003)$^+$
	T_A		1	25	0.006	0.002 (0.001)
	I_G		1	6.7	0.01	-0.078 (0.031)
	I_P capelin		1	23.5	< 0.0001	0.021 (0.004)
	I_P large invertebrates		1	5.4	0.02	0.008 (0.003)
8	Model	0.35	185	11.9	< 0.0001	0.034 (0.003)$^+$
	T_A		1	42.4	< 0.0001	-0.041 (0.006)
	I_P small invertebrate		1	12.7	< 0.0001	0.008 (0.002)
9	Model	0.52	176	22,5	< 0.0001	0.021 (0.007)$^+$
	T_A		1	8.1	0.005	-0.031 (0.011)
	I_P capelin		1	13.9	0.0003	0.017 (0.004)
	I_P small invertebrates		1	74.3	< 0.0001	0.041 (0.004)
	I_P demersal fishes		1	7.7	0.006	0.253 (0.091)

3.9 Figures

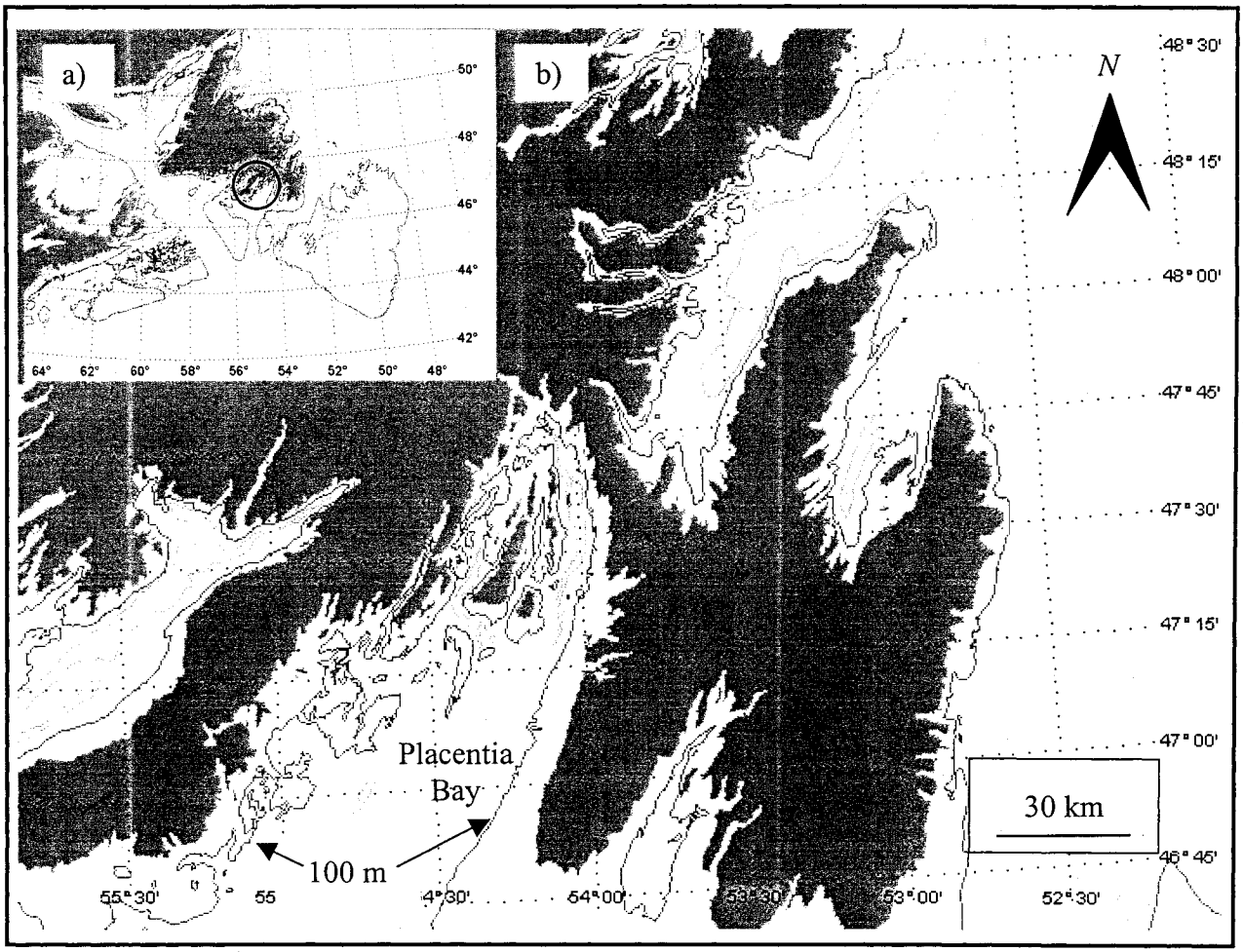

Figure 3.1 (a) East coast of North America showing Placentia Bay (inside circle) on the south coast of Newfoundland, Canada and (b) detailed view of the bay showing the 100 m depth contour (black arrow).

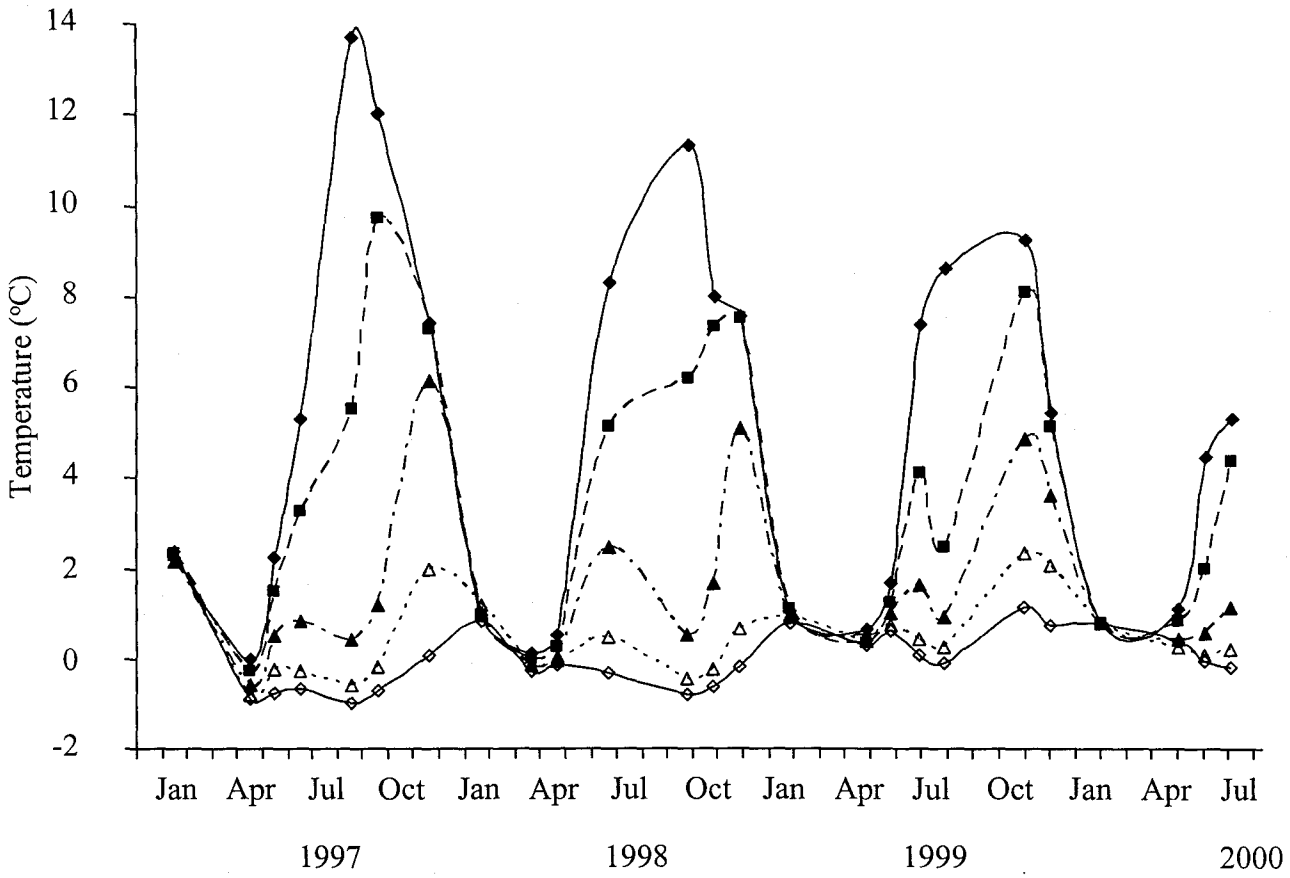

Figure 3.2 Mean water temperature (°C) at different depths in Placentia Bay. Depths: black diamond = 10 m, black square = 25 m, black triangle = 50 m, open triangle = 75 m, and open diamond = 100 m.

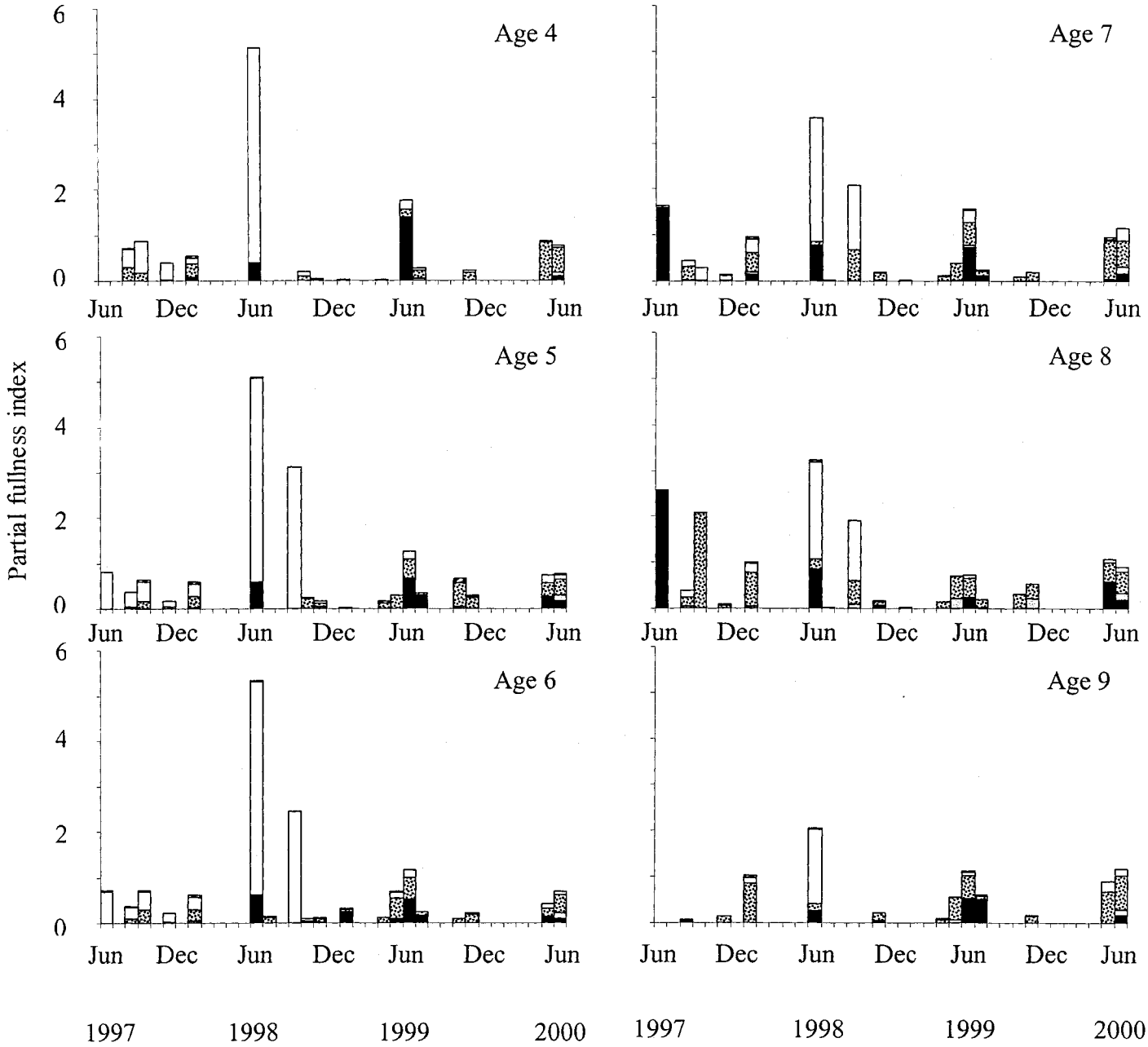

Figure 3.3 Mean partial fullness index (I_P) and total fullness index ($I_T = \Sigma I_P$) of cod ages 4-9. The I_P for prey groups whose relative contribution to cod diet was small were pooled for presentation purposes. ■ = capelin, ▒ = other fishes (sandlance, pelagic, demersal, and unidentified fishes), ▓ = large invertebrates, □ = small invertebrates and ▨ = other prey groups (algal material and unidentified prey).

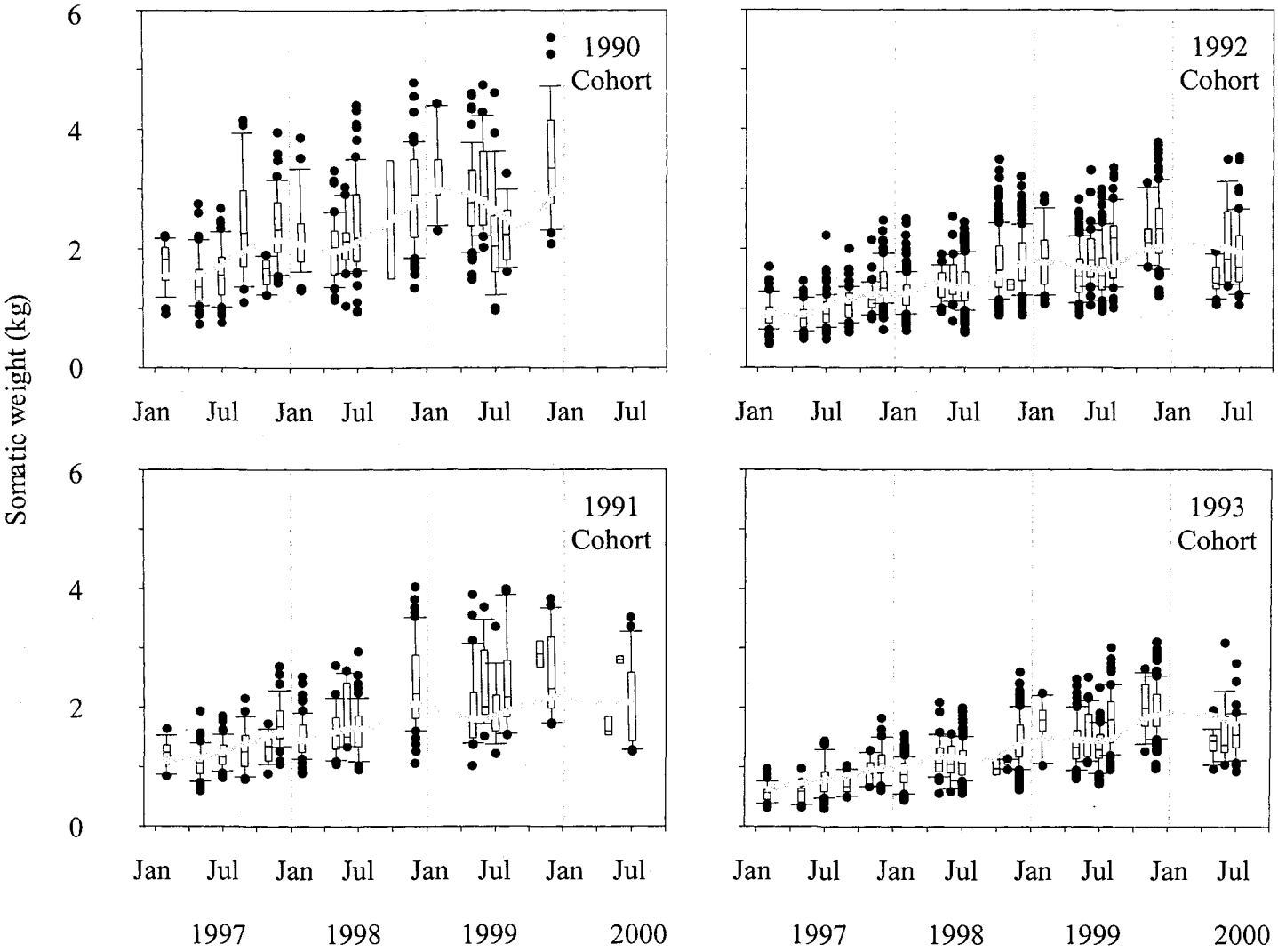

Figure 3.4 Box plots showing the somatic weight (raw data) and the mean predicted by the loess model (grey line) for cod sampled in Placentia Bay. Cohorts: 1990 (ages 7 to 9), 1991 (ages 6 to 9), 1992 (ages 5 to 8), and 1993 (ages 4 to 7). The grey box lower and upper limits represent the 1st and 3rd quartiles, respectively, the horizontal line inside the box represents the median and the lower and upper limits of the vertical bars represent the 10th and 90th percentiles, with values beyond this range represented by black dots.

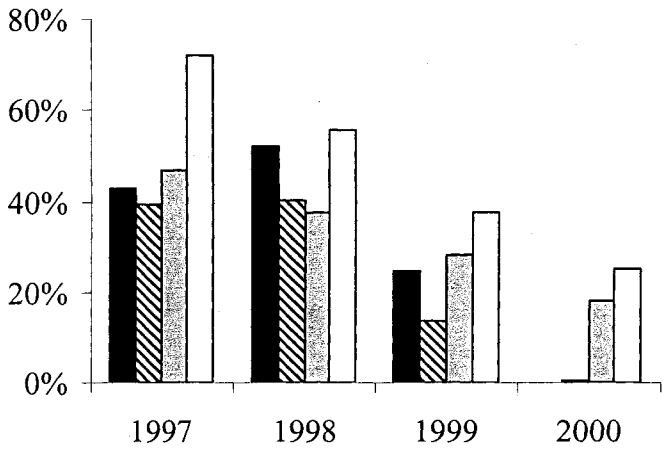

Figure 3.5 Inter-seasonal (spring-fall) variation in somatic weight of cod expressed as the percentage difference between the minimum and maximum mean weight predicted by the loess model for each age and year. Cohorts: ■ = 1990, ▨ = 1991, ▩ = 1992 and □ = 1993.

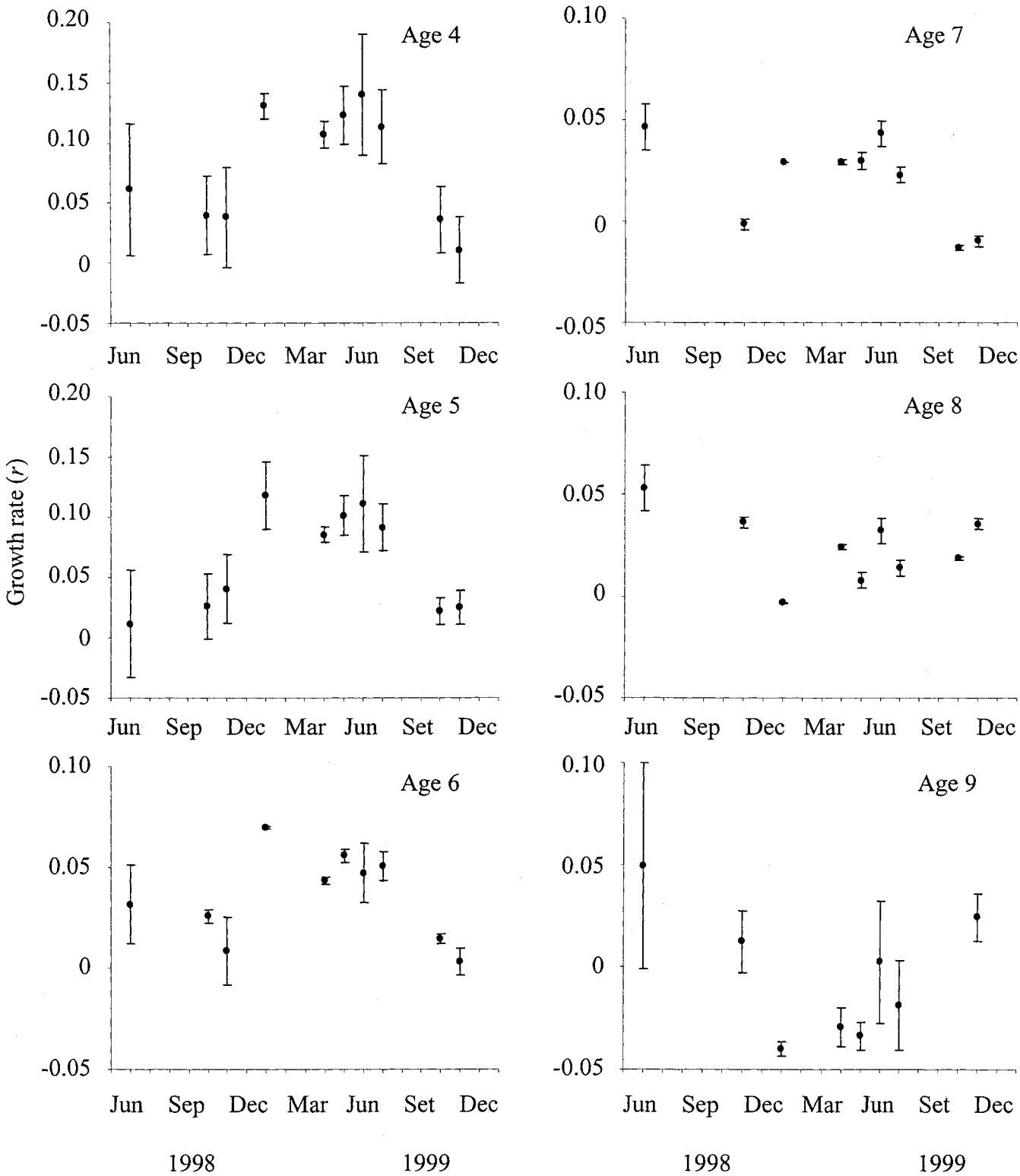

Figure 3.6 Growth rate (r) for Placentia Bay cod ages 4-9 estimated from linear regression models. The figures for cod ages 4-5 have a different y-axis scale from those observed for ages 6-9. Vertical T-bars represent ± SD.

Appendix 3.1 List of prey identified in cod stomachs sampled in Placentia Bay during 1997-2000.

Pisces	Decapode	Mollusca	Echinodermata	Coelenterata	Polychaeta	Amphipoda	Copepoda	Malacostraca	Chordata	Brachiopoda	Bryozoa	Hydrozoa	Isopoda	Porifera	Sipuncula	Unknown
Agonidae	Argis dentata	Aemaeidae	Asteroidea	Actinaria	Aphroditidae	Caprellidea	Copepoda	Euphasiacea	Ascidiacea	Brachiopoda	Bryozoa	Hydrozoa	Isopoda	Porifera	Sipunculidea	Actediellus sp
Agonus decagonus	Cancer sp	Bivalvia	Gorgonocephalidae			Gammaridea		Natantia	Pyuridae							Coffidae
Ammodytidae	Cancridae	Cephalopoda	Holothuroidea			Hyperiidae		Thysanoessa sp								
Anarhicadidae	Chionecetes opilio	Chlamys islandica	Ophiuroidea													
Anarhichas lupus	Crangonidae	Cyclocardia borealis	Psolus fabricii													
Artediellus sp	Crustacea	Echinarachinus parma	Strongylocentrotus sp													
Blennoidea	Eualus fabricci	Gastropoda														
Boreogadus saida	Eualus gaimardi	Illex illecebrosus														
Clupea harengus	Eualus macilentus	Invertebrate														
Cottidae	Eualus sp	Littorina sp														
Cryptacanthodes maculatus	Hyas araneus	Mya sp														
Cyclopteridae	Hyas coarctatus	Mytilidae														
Cyclopterus lumpus	Hyas sp	Nuculana sp														
Eumesogrammus praecisus	Lebbeus borealis	Octopoda														
Eumicrotremus spinosus	Lebbeus groenlandicus	Pectinidae														
Fish	Lebbeus microcerus	Solenidae														
Gadus morhua	Lebbeus polaris	Turbonilla sp														
Gaidropsarus ensis	Lebbeus sp															
Gasterosteidae	Majidae															
Gymnelus viridis	Mysidacea															
Hippoglossoides platessoides	Paguridae															
Hookear	Pandalus borealis															
Icelus bicornis	Pandalus montagui															
Icelus sp	Pandalus sp															
Icelus spatula	Reptantia															
Liparidae	Sabinea sarsi															
Liparis sp	Sabinea septemcarinata															
Lumpenus lumpretaeformis	Sabinea sp															
Lumpenus maculatus	Spirontocaris lilljeborgi															
Lumpenus sp	Spirontocaris phippsi															
Lycodes sp	Spirontocaris sp															
Macrourus berglax	Spirontocaris spinus															
Macrozoarces americanis																
Mallotus villosus																
Margarites sp																
Myctophidae																
Myoxocephalus scorpius																
Pholis gunnellus																
Pleuronectidae																
Reinhardtius hippoglossoides																
Sebastes sp																
Stichaeidae																
Triglops murrayi																
Triglops sp																
Urophycis chuss																
Urophycis tenuis																
Zoarcidae																

Chapter 4 Using geostatistics to quantify seasonal distribution and aggregation patterns of fishes: an example of Atlantic cod (*Gadus morhua*)

4.1 Abstract

Geostatistical methods were used to (1) quantify fish aggregation patterns over a range of scales (100 m to 67 km), using both simulated and acoustic density data of Atlantic cod (*Gadus morhua*) and (2) examine how changes in aggregation patterns influenced the precision of geostatistical density indices. Variogram parameters (range, sill and nugget) reflected changes in distribution patterns. Variograms of dispersed and low-density aggregations had large range, small sill and nugget values. In contrast, when fish were aggregated in a small portion of the study area the range was low and the sill and nugget large. The precision of density indices (CV) was below 20% in all cases, but maximum during summer when cod were broadly distributed in small, moderate to dense aggregations. Geostatistical modeling allowed describing and quantifying distribution patterns of fish density over different scales of observation, comparisons of spatio-temporal changes in density distribution and estimations of the precision of density indices while accounting for the effects of heterogeneous distributions, outliers and the typically large number of zero and low density observations. Geostatistical methods have particular applicability to fishes exhibiting gregarious behaviour and seasonally variable distributions, which includes many temperate and high-latitude fish species.

4.2 Introduction

Temperate water fishes typically exhibit changes in distribution and aggregation patterns at seasonal, annual and decadal time scales (Rose *et al.*, 2000; Vilhjálmsson 2002). Likewise, fish often exhibit contagious distribution in association with particular habitats (Imbrock *et al.*, 1996; Fréon and Misund, 1999), or behavioural changes for example during migrations, spawning and overwintering periods (Nøttestad *et al.*, 1996; Rose, 2003), growth and feeding cycles (Stoner and Abookire, 2002; Hovde *et al.*, 2002). Survey designs and analytical methods normally used in fisheries may not always be appropriate for assessing such distribution patterns of fish (MacLennan and Simmonds, 1992; Hanselman *et al.*, 2001) and invertebrates (Vining *et al.*, 2001) and have tended to rely on ad hoc measures to describe distributions and changes in spatially structured data (e.g., de Young and Rose, 1993; Hutchings, 1996).

Geostatistical methods were developed for spatially structured mining data during the 1960s (Matheron, 1963). Geostatistical methods are particularly relevant to serially correlated acoustic survey data because they do not require sample independence and have been used with pelagic fish (Simard *et al.*, 1993; Maravelias *et al.*, 1996), demersal fish (Williamson and Traynor, 1996; Rivoirard *et al.*, 2000), shellfish (Simard *et al.*, 1992; Maynou *et al.*, 1998) and plankton (Simard and Lavoie, 1999; Romaine *et al.*, 2002). The use of randomly positioned stations may lead to sample independence, but such methods tend to limit spatial resolution (Langton *et al.*, 1995). Geostatistical methods are commonly used for estimating patchness in fish distribution (Fréon and

Misund, 1999). However, there is a limited understanding about how geostatistical methods may be used to describe and quantify fish aggregations and its effects on the precision of acoustic density indices.

Atlantic cod (*Gadus morhua*) exhibit marked (seasonal to decadal) changes in distribution and aggregation patterns (Rose, 2003). Several methods have been used in attempts to quantify such patterns from trawl or acoustic survey data (e.g., Myers and Cadigan, 1995; Rose *et al.,* 2000). This study investigated the use of geostatistical methods to quantify seasonal distribution patterns over a broad range of scales from 100 m to approximately 70 km using both simulated and acoustic survey data. First conceptual models were developed using simulated data distributions and used to demonstrate the interaction of various distribution patterns with variogram parameters. These concepts were then applied to variograms estimated from cod surveys conducted in Placentia Bay, Newfoundland during 1999 and results discussed in relation to season, habitat and migration patterns. Effects of the distribution patterns on the precision of the acoustic density indices were also examined.

4.3 Material and Methods

4.3.1 Area of study

Placentia Bay is a large embayment (132 km x 100 km) on the south coast of Newfoundland (Figure 4.1). Based on topographic and bathymetric features the bay was

divided in two components (inner and outer bay) or strata. The inner bay is divided by a series of islands into three deep channels that merge to form a deep basin (outer bay), which extends from the bay into the offshore. Placentia Bay remains ice-free year-round, except for areas near strong fresh water inflows. Depths in the western channel reach 450 m while the eastern and central channels have maximum depths of 375 m. The bottom topography is rugged and variable (Willey, 1976), particularly in the inner bay and the sediment types vary markedly over small distances (Stehman, 1976).

4.3.2 Acoustic surveys

Five acoustic surveys were conducted in Placentia Bay between April and November 1999 (Table 4.1). Surveys were run over relative short periods of time (8-29 days) in order to minimise the effects of temporal (intra-seasonal) variability caused by changes in fish distribution and movement. The surveys employed a BioSonics DT 4000 echosounder with 120 kHz transducer mounted on a towed body. The system was calibrated in situ with a tungsten-carbide standard target (Foote *et al.*, 1987).

Areas of the bay between 10-120 m depth were stratified into 28 blocks (1 block = 120 km^2, Figure 4.1). Earlier work had shown that cod are uncommon at depths greater then 100 m in Placentia Bay from spring to fall (Lawson and Rose, 1999). Block size was chosen based on logistic considerations such as the survey area covered in a day, including acoustic and biological sampling (2-3 blocks per day) and the total number of days available for surveying. Contiguous blocks were allocated across the study area,

starting at the inner most region of the bay. For each block, transects were run during daytime period only (maximum hydro-acoustic detectability. See Lawson and Rose, 1999) along lines of latitude with start position randomly selected. This coverage was then followed by a more intense acoustic sampling (approximately 0.5 km equally spaced parallel transects) in areas where cod aggregations were found (both strata). Such aggregations were typically dense (0.1-1 fish.m^{-2}) and small (< 1 km in length). The overall transect distance covered in each block was in most cases the same (11 km), but transect selection within blocks depended on the topographic and bathymetric features of the area surveyed and navigational obstacles (e.g. shoals, fishing gears), resulting in many cases of a series of short transects. Most blocks were covered during each survey, except in April. However, when and where blocks were surveyed was dictated primarily by the weather conditions at the time.

Acoustic data (echograms) were edited manually and integrated using FASIT software (Lefeuvre *et al.,* 2000) to determine an area backscattering coefficient for each 100 m. Fish density (fish.m^{-2}) was estimated as:

$$fish\ density = s_a . \theta_{bs}^{-1} . D^{-1} \quad (1)$$

where s_a is area backscattering coefficient ($m^2.m^{-2}$), Θ_{bs} is the arithmetic mean acoustic backscattering cross section of one fish (e.g., $\theta_{bs} = 10^{\frac{TS}{10}}$) and D is detectability. Detectability was determined in independent experiments (Lawson and Rose, 1999). Target strength (TS) was estimated as:

TS (dB) = 20 log (length (cm)) - 67.5 (Rose and Lawson, 1999; Rose, 2003) (2)

For each block, the raw acoustic densities were averaged over each minute of latitude and two minutes of longitude, which at latitude 47° N (study area) is roughly equivalent to an area of 3.5 km^2. This procedure standardised sampling effort, while preserving the spatial structure of the data. Averaging data over regular distance intervals is a common procedure in fisheries acoustics (MacLennan and Simmonds, 1992; Rivoirard *et al.*, 2000; Rose, 2003). One reason is because acoustic data are recorded continuously along the survey transects and integrated over short distance intervals (in this case for each 100 m), generating very high number of observations. There are no general rules about averaging data over distance or area and for this study it was based on (1) the spatial scales of the surveyed areas (block and stratum), (2) sampling design, (3) computational efficiency to perform analyses and (4) the author understanding about biological effects of cod aggregation in Placentia Bay (e.g., aggregation patterns and cod behaviour during spawning or feeding periods). The approach used reduced (i.e., smoothed) to some extent the variability of the data, but the scale used to average the data (3.5 km^2) is small enough to preserve the spatial structure of the data while considering the four points as listed above.

Next, fish density indices (mean fish density per stratum) and coefficient of variation (CV) for each survey and stratum were estimated using geostatistics. Biological samples were obtained in all surveys from cod aggregations identified acoustically. Fishing sets

used four handlines with six equal size unbaited hooks (10.2 cm long by 2.6 cm wide) fished for 30 minutes. A total of 1090 fish were sampled for length (cm). Mean length per 4-cm class interval was calculated and used for estimating the acoustic target strengths (Equation 2), which were used to obtain fish density estimates.

4.3.3 Geostatistics

In geostatistical methods the spatial variability of the data is modeled as auto-correlation and incorporated into the estimation procedure by weighting the sample values with the appropriate variogram model (Matheron, 1963). The variogram is the main tool of geostatistics and measures the spatial correlation by describing how the data are related over distance and direction. In the case of gregarious fish, acoustic density data are typically characterised by many small and a few large values (Rivoirard *et al.,* 2000), which can significantly impact the variogram pattern and parameters (Krige and Magri, 1982). Therefore, a robust estimator of the variogram (Cressie and Hawkins, 1980) was used:

$$\bar{\gamma}(h) = \frac{\left\{ \frac{1}{2|N(h)|} \sum_{N(h)} |z_i - z_j|^{\frac{1}{2}} \right\}^4}{0.457 + 0.494/|N(h)|} \qquad (3)$$

where N(h) is the set of all pairwise distances i - j = h in a two dimensional plan, |N(h)| is the number of distinct pairs in N(h), z_i and z_j are data values at spatial locations i and j, respectively, 0.457 and 0.494 are model coefficients.

The geostatistical analysis consisted in evaluating stationarity, estimation of empirical variograms, fitting a theoretical variogram model and calculating predictions and standard deviation of the unknown values using kriging (Matheron, 1971) as an extrapolation method. The spatial stationarity assumption implies a process with a constant mean and with the variance defined only as a function of distance and not location (Cressie, 1993). Directional variograms were used to check for the presence of trend in the data, anisotropy in variograms, or some other form of non-stationarity. Multiple directional variograms were computed by specifying a vector of azimuths (0^0, 15^0,..., 135^0). Variograms considered only distances h for which $|N(h)| > 30$ (Journel and Huijbregts, 1978). When detected trends were removed from the data by a linear transformation using the residuals of local regression or Loess model (Cleveland and Devlin, 1988). Directional variograms were computed and compared using loess models to fit and remove trends from the data using latitudinal and longitudinal distances across the sampling area as predictors. The variograms were then estimated using these corrected locations. Details on this technique may be found in Journel and Huijbregts (1978).

Geometric anisotropy (i.e., variogram range varies with direction) was detected in some cases and empirical variograms were calculated based on the appropriate correction, that is incorporating the detected direction of anisotropy in the variogram model and generate an equivalent isotropic model. All geostatistical analyses were performed using S+ Spatial Stats software (Insightful Corporation). The resulting empirical variograms were then fitted with appropriate theoretical variogram models. The initial model fitting was

done manually based on the shape of the empirical variogram. Spherical, exponential, gaussian and power models (Cressie, 1993; Rivoirard *et al.,* 2000) were fitted. Variogram parameters were modified and the results overlaid onto the empirical variogram until a satisfactory fit was obtained. The final model was chosen based on the measurement of model fit that minimizes the objective function $\sum_{h}\left[\gamma(h)-\gamma^{*}(h)\right]^{2}$, that is the residual sum of squares between the theoretical and empirical variograms $\gamma(h)$ and $\gamma^{*}(h)$, respectively (Cressie, 1993). In all cases, spherical models with or without a nugget term provided the best fit (i.e., minimizes the objective function). Nugget refers to the micro-scale variations of data that are not described by spatial scale. The model is:

$$\gamma(h)=c\left[\frac{3|h|}{2a}-\frac{|h|^{3}}{a^{3}}\right], \qquad \text{for } |h| < a \qquad (4)$$

$$\gamma(h)=c, \qquad \text{for } |h| \geq a \qquad (5)$$

where c is the sill of the variogram $\gamma(h)$ representing the maximum level of variability in data measurements, $|h|$ is the scalar distance between two measurements and a is the range of the variogram $\gamma(h)$ and represents the distance at which data are no longer correlated. The nugget model used was:

$$\gamma(h) = 0 \qquad \text{for } h = 0 \qquad (6)$$

$$\gamma(h) = c \qquad \text{for } |h| > 0 \qquad (7)$$

Ordinary kriging was used to interpolate unsampled locations based on the theoretical variogram weighted by a linear combination of available samples. Ordinary kriging allows incorporating a model of the covariance when estimating predictions. Kriging predictions were computed as:

$$Z(V) = \sum_{i=1}^{N} \lambda_i Z(x_i) \qquad (8)$$

where Z(V) is the estimate of density at an unsampled point, N is the number of samples, λ_i is the weight attributed to sample x_i. The use of weights ensures that the average error model is zero and the error variance is minimised (Isaaks and Srivastava, 1989). The kriging output included the location (latitude and longitude), predictions (fish.m^{-2}) and the standard deviation of the predictions. The precision of the estimates was obtained by calculating the coefficient of variation (CV).

Next, the use the variogram parameters range, sill and nugget as quantitative indicators of distribution and aggregation patterns of fish were investigated using both simulated and acoustic density data of cod. In the case of variogram models described by asymptotic functions such as the spherical or gaussian models, the nugget is the y-intercept, while the range and sill are both determined by the upper inflexion point where the line becomes flat. The x co-ordinate of this inflexion point is the range while the y co-ordinate is the sill. In practical terms, nugget represents the micro-scale variation of data and/or possible measurement errors. That is variability smaller than the sampling unit distance, so appearing as an effect not explained by spatial scale. The variogram range can be thought

of as an indicator of the size of aggregations such as fish schools or cluster of schools (Petitgas, 1993; Maravelias *et al.,* 1996; Fréon and Misund, 1999) and the sill corresponds to the extent of the variance related to spatial scale (Hanselman *et al.,* 2001), and hence an indicator of the degree of variability in auto-correlated data such as acoustic density measurements.

4.3.4 Aggregation types

There are varying views about what comprises a fish school. Breder and Halpern (1946) defined schools as groups of fish equally oriented, regularly spaced and with similar swimming speed and Radakov (1973) simply as a group of fish swimming together. Fréon and Misund (1999) considered a fish school as a functional unit and Petitgas *et al.* (2001) as discrete events in space. Also, the size of schools and clusters of schools vary greatly. Fréon *et al.* (1992) observed that a school of *Harengula clupeola* varied between 145-522 m^2 in one hour period and Maravelias *et al.* (1996) observed Atlantic herring (*Clupea harengus*) schools over distances of 12 km. Similarly, clusters of schools have been reported to reach lengths of 55 km for walleye pollock (*Theragra chalcogramma*) (Sullivan, 1991) or larger for tunas (Fréon and Misund, 1999). Reid *et al.* (2000) suggested that morphometric (e.g., length, area), energetic (e.g., acoustic backscattering), and positional parameters (e.g., latitude/longitude, depth) could be used to characterise fish schools and clusters of schools. In this study, the definition of aggregation type was based on (1) morphological and energetic parameters: density estimates and size of aggregations based on acoustic data analysis and integration and (2) empirical approach

based on the author knowledge of biological/behavioural effects of cod aggregation in Placentia Bay. Using these criteria three types of aggregations were identified (1) fish schools, single dense (0.1-1 fish.m^{-2}) and small (< 2 km) groupings of fish, (2) clusters of schools (≥ 2 km) and (3) large (> 25 km) and low-density aggregations (< 0.01 fish.m^{-2}).

4.3.5 Conceptual models

Conceptual models for interpreting spatial structure through variogram parameters were developed using simulated data. The simulations produced measurements of aggregation size and spatial variability in data samples. The spatial patterns used in the simulations were arbitrarily chosen, but believed to encompass spatial distributions observed for most fish populations. In general terms, the spatial distribution of a population can follow three basic types: random, regular and contagious (Elliott, 1977) and the simulated data incorporated such distribution patterns. Co-ordinated two-dimensional data (e.g., arbitrary unit (au) = number of fish.surface $unit^{-1}$) consisting of 2500 locations (1 au x 1 au grid) were generated using an ordinary spreadsheet package. For each scenario sample values consisting of 95% zero and low values were randomly selected from a normal distribution ranging from 1 to 10,000 and the remaining values from 10,001 to 30,000. Scenarios containing aggregations were created with either (1) relatively low variability in sample values within aggregations (values were randomly selected from a normal distribution ranging from 50,000 to 100,000), (2) high variability in sample values (12,000 to 1,000,000) and (3) an equally spaced and uniform values of 100,000. The

locations and size of aggregations were arbitrarily selected with aggregation size varying from 100 (au^2) to 750 (au^2).

4.4 Results

4.4.1 Conceptual models

The simulations showed that when fish were randomly distributed (Figures 4.2a and 4.2b) the variogram tended to be flat indicating only a nugget effect. The size of the nugget was dependent on the amount of sample variability. Nugget was relatively smaller when variability in sample values was low (Figure 4.3a), but increased as variability in samples increased (Figure 4.3b).

Alternatively, in scenarios containing contagious distribution, $\gamma(h)$ increased with distance then levelled off where correlation with distance approached zero (range). The range, sill and nugget values depended on the size, number, and proximity of aggregations and the degree of variability in sample values within aggregations. In the case of a large aggregation (15 au x 50 au) with low variability in sample values across the aggregation (Figure 4.2c), the variogram exhibited relatively large range (50 au), small sill (3.10^7 au^2) and no nugget effect (Figure 4.3c). When the variability in sample values increased (Figure 4.2d), a comparable increase in sill was observed (7.10^8 au^2, Figure 4.3d).

Smaller and denser neighbouring aggregations (Figures 4.2e and 4.2f), varying each from approximately 10 au x 10 au to 20 au x 20 au resulted in smaller range (42-44 au) and larger sill (2.10^9 au^2) and nugget effect varied from 2.10^5 au^2 to 10^6 au^2, Figures 4.3e and 4.3f). In these simulations, the variogram range and sill reflected cluster size and a larger spatial heterogeneity in sample values rather than the spatial properties of any single aggregation.

The scenarios where most large sample values were distributed within a small portion of the area (10 au x 18 au, Figures 4.2g and 4.2h) resulted in the smallest ranges (14 au), the largest sill (3.10^9 au^2) and nugget values (3.10^8 au^2, Figures 4.3g and 4.3h). In contrast, the smallest sill value (7.10^6 au^2) was observed for the scenario containing uniformly distributed samples within aggregations, reflecting low spatial variability in samples values (Figures 4.2i and 4.3i).

4.4.2 Cod data

In all periods, fish densities were characterised by a large dispersion of values (3 orders of magnitude) and skewed frequency distributions with many low and a few high values (Figure 4.4). In April and May most cod were found in a few dense aggregations ($\geq$ 0.1 $fish.m^{-2}$) in the inner bay and on the east side of the bay to Cape St. Mary's (May) (Figures 4.5a and 4.5b). By July, cod were more dispersed in moderate to dense aggregations ($\geq$ 0.01 $fish.m^{-2}$, Figure 4.5c). A similar distribution pattern predominated in October, although fewer cod were located over the outer bay banks (Figure 4.5d). In

November, dense aggregations again formed at the head of the bay and low cod densities (< 0.01 fish.m^{-2}) were observed in the outer bay (Figure 4.5e). Higher proportions of dense aggregations were found in July and November.

Variograms were determined for each survey and stratum to address inter-seasonal differences in fish distribution. All variograms showed evidence of spatial structure (Figure 4.6), although non-random dispersion of points around the theoretical variogram was observed in some cases (November). Variogram range varied between 9-67 km and was higher in the outer than inner bay in all months except October. Variogram sill varied between 10^{-9} and 3.10^{-5} (fish.m^{-2})^2 and was lower in the outer than inner bay in all months. Nugget effect was observed in several variograms. Large nugget effect occurred in the inner bay in April, May and November (20-27% of the sill). However, overall the nugget effect was low (< 8% of the sill).

Kriged cod density indices increased from April to July in the inner bay, from 0.003 to 0.015 fish.m^{-2} and from 0.001 to 0.003 fish.m^{-2} in the outer bay (Table 4.2). Density indices decreased between July and October, particularly in the inner bay, to 0.001 fish.m^{-2} and then increased in November to 0.004 fish.m^{-2}. Overall, indices were higher in the inner bay in all periods except in October. CVs varied between 5% in July in the inner bay and 19% in May and October in the outer and inner bay, respectively.

4.5 Discussion

The simulations and analyses of fish density distribution show that variogram parameters provide an effective way of describing and quantifying fish aggregations at different scales of observation, as well as examining the effect of changes in aggregation patterns to the precision of density indices. In the case of cod density distribution the variogram range, sill and nugget reflected changes in distribution patterns over the surveyed area, consistent with those observed in the simulated data. In both analyses, variograms of low density and large aggregations were characterised by large range, and small sill and nugget values. In the cod surveys such a scenario occurred in the outer bay when cod were distributed over larger aggregations (range > 42 km) and densities ≤ 0.001 fish.m^{-2}, particularly in April and May. However, when most fish were located in relative small portions of the study area (large spatial heterogeneity in sample values), range was small and sill and nugget values were large, as seen in variograms for the inner bay in April, May and November when cod were found in denser (up to 0.008 fish.m^{-2}) and smaller aggregations (range < 22 km).

Marine habitats often contain directional gradients with which fish might be associated (Swartzman *et al.,* 1999; Maravelias et. al., 2000). In the case of Placentia Bay cod the differences in distribution between the inner and the outer bay may relate in part to the scale of habitat complexity. The inner bay is characterised by complex small-scale bathymetric features, with semi-enclosed embayments, deep channels and shallow banks,

whereas the outer bay bathymetry is simpler and characterised by a short shelf and a deep basin extending to the offshore.

The observed fish distribution patterns may also relate to spawning (April-May), feeding cycles (July) and seasonal migrations (Davis *et al.,* 1994; Lawson and Rose, 2000; Robichaud and Rose, 2001; Mello and Rose, 2005a). Variograms for the inner bay tended to have smaller ranges throughout the year, suggesting that habitat may be a limiting factor in this case. Of note, sill and nugget values increased sharply in the pre-overwintering period (November) as fish concentrated into a small area of the bay, behaviour similar to that observed in Smith Sound, Trinity Bay, on the Northeast Newfoundland coast (Rose, 2003). By contrast, in the outer bay, there is little variation in sill and nugget in July, October and November, but variogram ranges differ. This may reflect a lack of preferred habitat coupled with a positive relation between the percentage of habitat utilised and abundance.

The precision of the geostatistical density indices (CVs) was in every case below the maximum level of variability (25%) suggested by Pope (1982) as necessary to produce stock assessments and calculate a total allowable catch (TAC) with acceptable confidence limits. However, changes in aggregation patterns had important effects in the precision of density indices. For example, CVs declined when fish were highly aggregated in November (14-17%), whereas the smallest CVs (5-8%) were observed in July when cod were more dispersed in small, moderate to dense aggregations throughout the study area.

Regarding the adequacy of the surveys and the precision of abundance estimations, the July indices may not represent accurately the local (spawning) stock abundance. Previous studies (Davis *et al.,* 1994; Lawson and Rose, 2000) indicated that cod from adjacent stocks move into the bay mostly during the post spawning and summer seasons and mixing with local fish. The index was higher in the outer bay in October suggesting that the stock was broadly dispersed through the bay during this period. The November survey indices likely reflected stock abundance more accurately, as most local cod are believed to be present in the bay at this time of the year preparing for overwintering (Mello and Rose, 2005b). Also, the differences in indices between October and November suggest an important shift in distribution from the outer bay to the inner bay in a relatively short period of time (< 21 days).

Surveying during periods when the stock is highly aggregated is favourable to survey designs such as the one employed in this study, because most stock biomass could be easily and cost effectively covered and suitable for replicated surveys and further improvement of estimates of variability in survey data (Romaine *et al.*, 2002; Rose, 2003). Some points of concern include surveying during the peak of the commercial fishery (Brattey *et al.,* 2002) and also the possibility of rough fall weather, which may affect the quality of acoustic data.

Previous techniques used to analyse spatial distribution patterns of fish include Taylor's power law model (Gauthiez, 1997), negative binomial distribution models (Welsh and Ishida, 1993; Jarvela and Thorsteinson, 1999), density composition and nested

aggregation models (Hutchings, 1996), cluster analysis (Magill and Sayer, 2002), geostatistical aggregation curves (Petitgas, 1998) and linear models applied to commercial catch rates (Vignaux, 1996). These techniques are often (1) dependent on assumptions such as constant density, abundance or area of population distribution (Langton *et al.,* 1995; Petitgas, 1998), (2) limited by the size of the sampling unit or scale of observation (Elliott, 1977) and (3) dependent on the understanding of functional relationships of model parameters (Booth, 2000). For example, indices of spatial pattern such as Taylor's power law b index and the negative binomial k index are based on the relationship between the variance and mean of the observations measured. Hence, these indices should only be used to compare distributions when the sample mean, the total number of individuals in the sample and number of sampling units are similar. In practice, these assumptions are often difficult to meet and indices based on the variance to mean ratio may not represent a good measure of the degree of aggregation in a population (Elliott, 1977).

Previous studies based on geostatistical analysis have related the variogram parameters to the scale and spatial variability of fish aggregations. Petitgas and Levenez (1996) related the variogram range and sill to the dimensions and the number of clusters of pelagic schools per sampling unit area, respectively. Variogram range has been used as an indicator of cluster size for both demersal and pelagic fish schools (Sullivan, 1991; Petitgas, 1993). Maravelias *et al.* (1996) implicitly related the size of Atlantic herring aggregations to different range values, by suggesting that meso-scale values (12 km) represented herring schools and larger range values (37 km) represented larger scale

aggregations. Bez and Rivoirard (2001) used variogram parameters to describe the spatial structure and identify the different scales of mackerel (*Scomber scombrus*) ichthyoplankton aggregations. The findings of this study concur with the results of these studies, but extend them by developing a conceptual framework to interpret the properties variogram parameters.

In conclusion, geostatistical modeling allowed describing and quantifying distribution patterns of fish density over different scales of observation, comparisons of the temporal and spatial changes in density distribution and estimations of the precision of fish density indices while accounting for the effects of heterogeneous distributions, outliers and the typically large number of zero and low density observations. Geostatistical methods have particular applicability to fishes exhibiting gregarious behaviour and seasonally variable distributions, which includes many temperate and high-latitude fish species such as Atlantic cod.

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4.7 References

Bez, N., and Rivoirard, J. 2001. Transitive geostatistics to characterise spatial aggregations with diffuse limits, an application on mackerel ichthyoplankton. Fisheries Research, 50: 41-58.

Booth, A.J. 2000. Incorporating the spatial component of fisheries data into stock assessment models. ICES Journal of Marine Science, 57: 858-865.

Brattey, J., Cadigan, N.G., Healey, B.P., Lilly, G.R., Murphy, E.F., Shelton, P.A., Stansbury, D.E., Morgan, M.J., and Mahé, J.-C. 2002. An assessment of the cod (*Gadus morhua*) stock in NAFO Subdivision 3Ps in October 2002. DFO Canadian Science Advisory Secretariat Research Document 2002/96.

Breder C.M., and Halpern, F. 1946. Innate and acquired behaviour affecting the aggregation of fishes. Physiological Zoology, 19: 154-190.

Cleveland, W.S., and Devlin, S.J. 1988. Locally-weighted Regression: An approach to regression analysis by local fitting. Journal of the American Statistical Association, 83: 596-610.

Cressie, N.A.C., 1993. Statistics for spatial data. John Wiley & Sons, Inc. New York.

Cressie, N., and Hawkins, D.M. 1980. Robust estimation of the variogram. Mathematical Geology, 12: 115-125.

Davis, M. B., P. Lundrigan and R. Ripley 1994. A description of cod stock structure in Placentia Bay, NAFO Subdivision 3Ps. DFO Atlantic Fisheries Research Document 94/32.

de Young, B., and Rose, G.A. 1993. On recruitment and distribution of Atlantic cod (*Gadus morhua*) off Newfoundland. Canadian Journal of Fisheries and Aquatic Sciences, 50: 2729-2741.

Elliott, J.M. 1977. Some methods for the statistical analysis of samples of benthic invertebrates. Freshwater Biological Publication No. 25.

Foote, K.G., Knudsen, H.P., and Vestnes, G. 1987. Calibration of acoustic instruments for fish density estimation: a practical guide. ICES Co-operative Research Report No. 144.

Fréon, P., and Misund, O.A. 1999. Dynamics of pelagic fish distribution and behaviour: effects on fisheries and stock assessment. Blackwell Science, Cambridge.

Fréon, P., Gerlotto, F., and Soria, M. 1992. Changes in school structure according to external stimuli: description and influence on acoustic assessment. Fisheries Research, 15: 45-66.

Gauthiez, F. 1997. Structuration spatiale des populations de poissons marins démersaux. Thèse de Doctorat, Université Claude Bernard Lyon I, France, 297 pp.

Hanselman, D.H., Quinn, T.J., Heifetz, J., Clausen, D. and Lunsford, C. 2001. Spatial inferences from adaptive cluster sampling of Gulf of Alaska Rockfish. *In* Kruse, G.H., Bez, N., Booth, A., Dorn, M.W., Hills, S., Lipcius, R.N., Pelletier, D., Roy, C., Smith, S.J., and Witherells, D. (eds), Spatial processes and management of marine populations. Lowell Wakefield Fisheries Symposium Series, 17: 303-325.

Hovde, S.C., Albert, O.T., and Nilssen, E.M. 2002. Spatial, seasonal and ontogenetic variation in diet of Northeast Arctic Greenland halibut (*Reinhardtius hippoglossoides*). ICES Journal of Marine Science, 59: 421-437.

Hutchings, J.A. 1996. Spatial and temporal variation in the density of northern cod and review of hypotheses for the stock's collapse. Canadian Journal of Fisheries and Aquatic Sciences, 53: 943-962.

Imbrock, F., Appenzeller, A., and Eckmann, R. 1996. Diel and seasonal distribution of perch in Lake Constance: a hydroacoustic study and in situ observations. ICES Journal of Marine Science, 49: 1-13.

Isaaks, E.H., and Srivastava, R.M. 1989. Applied geostatistics. Oxford University Press, New York.

Jarvela, L.E., and Thorsteinson, L.K. 1999.The epipelagic fish community of Beaufort Sea coastal waters, Alaska. Arctic, 52: 80-94.

Journel A.G., and Huijbregts, C.J. 1978. Mining geostatistics. Academic Press, London.

Krige, D.G., and Magri, E.J. 1982. Studies on the effects of outliers and data transformation on variogram estimates for a base metal and a gold ore body. Mathematical Geology, 14: 557-564.

Langton, R.W., Auster, P.J., and Schneider, D.C. 1995. A spatial and temporal perspective on research and management of groundfish in the northwest Atlantic. Reviews in Fisheries Science, 3: 201-229.

Lawson, G.L., and Rose, G.A. 2000. Seasonal distribution and movements of coastal cod (*Gadus morhua*) in Placentia Bay, Newfoundland. Fisheries Research, 49: 61-75.

Lawson, G.L., and Rose, G.A. 1999. The importance of detectability to acoustic surveys of semi-demersal fish. ICES Journal of Marine Science, 56: 370-380.

Lefeuvre, P., Rose, G.A., Gosine, R., Hale, R., Pearson, W., and Khan, R. 2000. Acoustic species identification in the Northwest Atlantic using digital image processing. Fisheries Research, 47: 137-147.

MacLennan, D.N., and Simmonds, E.J. 1992. Fisheries acoustics. Chapman and Hall, London.

Magill, S.H., and Sayer, M.D.J. 2002. Seasonal and interannual variation in fish assemblages of northern temperate rocky subtidal habitats. Journal of Fish Biology, 61: 1198-1216.

Maravelias, C.D., Reid, D.G., and Swartzman, G. 2000. Modelling spatio-temporal effects of environment on Atlantic herring, *Clupea harengus*. Environmental Biology of Fishes, 58: 157-172.

Maravelias, C.D., Reid, D.G., Simmonds, J., and Haralabous, J. 1996. Spatial analysis and mapping of acoustic survey data in the presence of high local variability: geostatistical application to North Sea herring (*Clupea harengus*). Canadian Journal of Fisheries and Aquatic Sciences, 53: 1497-1505.

Matheron, G. 1971. The theory of regionalized variables and its applications. Cahiers du Centre de Morphologie Mathématique de Fontainbleau, Vol. 5.

Matheron, G. 1963. Principles of geostatistics. Economic Geology, 58: 1246-1266.

Maynou, F.X., Sarda, F., and Conan, G.Y. 1998. Assessment of the spatial structure and biomass evaluation of *Nephrops norvegicus* (L.) populations in the northwestern Mediterranean by geostatistics. ICES Journal of Marine Science, 55: 102-120.

Mello, L.G.S., and Rose, G.A. 2005a. Seasonal growth of Atlantic cod (*Gadus morhua* L.): effects of temperature, feeding and reproduction. Journal of Fish Biology, 67: 149-170.

Mello, L.G.S., and Rose, G.A. 2005b. Seasonal variation in abundance and stock composition of Atlantic cod (*Gadus morhua* L.) in Placentia Bay, Newfoundland, in relation to fisheries. Fisheries Research, 74: 142-156.

Myers, R.A., and Cadigan, N.G. 1995. Was an increase in natural mortality responsible for the collapse of northern cod? Canadian Journal of Fisheries and Aquatic Sciences, 52: 1274-1285.

Nøttestad, L, Aksland, M., Beltestad, A., Fernö, A., Johannessen, A., and Misund, O.A. 1996. Schooling dynamics of Norwegian spring spawning herring (*Clupea harengus L.*) in a coastal spawning area. Sarsia, 80: 277-284.

Petitgas, P., Reid D., Carrera, M. Iglesias, J. Georgakarakos, S. Liorzou, B., and Massé, J. 2001. On the relation between schools, clusters of schools, and abundance in pelagic fish stocks. ICES Journal of Marine Science, 58: 1150-1160.

Petitgas, P. 1998. Biomass-dependent dynamics of fish spatial distributions characterized by geostatistical aggregation curves. ICES Journal of Marine Science, 55: 443-453.

Petitgas, P., and Levenez, J.J. 1996. Spatial organization of pelagic fish: echogram structure, spatial-temporal condition, and biomass in Senegalese waters. ICES Journal of Marine Science, 55: 147-153.

Petitgas, P. 1993. Geostatistics for fish stock assessment: a review and acoustic application. ICES Journal of Marine Science, 50: 285-298.

Pope, J.G. 1982. Shortcut formulae for the estimation of coefficient of variation of status quo TAC's. ICES CM 1982/G:12.

Radakov, D.V. 1973. Schooling in the ecology of fish. John Wiley & Sons, New York.

Reid, D., Scalabrin, C., Petitgas, P., Massé, J., Aukland, R., Carrera, P., and Georgakarakos, S. 2000. Standard protocols for the analysis of school based data from echo sounder surveys. Fisheries Research, 47: 125-136.

Rivoirard, J., Simmonds, J., Foote, K.G., Fernandes, P., and Bez, N. 2000. Geostatistics for estimating fish abundance. Blackwell Science, Cornwall.

Robichaud, D., and Rose, G.A. 2001. Multiyear homing of Atlantic cod to a spawning ground. Canadian Journal of Fisheries and Aquatic Sciences, 58: 2325-2329.

Romaine, S.J., Mackas, D.L., and Macaulay, M.C. 2002. Comparison of euphausiid population size estimates using replicated acoustic surveys of coastal inlets and block average vs. geostatistical spatial interpolation methods. Fisheries Oceanography, 11: 102-115.

Rose, G.A. 2003. Monitoring coastal northern cod: towards an optimal survey of Smith Sound, Newfoundland. ICES Journal of Marine Science, 60: 453-462.

Rose, G.A., deYoung, B., Kulka, D.W., Goddard, S.V., and Fletcher, G.L. 2000. Distribution shifts and overfishing the northern cod (*Gadus morhua*): a view from the ocean. Canadian Journal of Fisheries and Aquatic Sciences, 57: 644-663.

Rose, G.A., and Lawson, G.L. 1999. Acoustic surveys in Placentia Bay and 3Ps, June 1996-1998. Canadian Stock Assessment Secretariat Research Document 99/41.

Simard, Y., and Lavoie, D. 1999. The rich krill aggregation of the Saguenay-St. Lawrence Marine Park: hydroacoustic and geostatistical biomass estimates, structure, variability, and significance for whales. Canadian Journal of Fisheries and Aquatic Sciences, 56: 1182-1197.

Simard, Y., Marcotte, D., and Bourgault, G. 1993. Exploration of geostatistical methods for mapping and estimating acoustic biomass of pelagic fish in the Gulf of St. Lawrence: size of echo-integration unit and auxiliary environmental variables. Aquatic Living Resources, 6: 185-199.

Simard, Y., Legendre, P., Lavoie, G., and Marcotte, D. 1992. Mapping, estimation biomass, and optimizing sampling programs for spatially autocorrelated data: case study of the northern shrimp (*Pandalus borealis*). Canadian Journal of Fisheries and Aquatic Sciences, 49: 32-45.

Stehman, C.F. 1976. Pleistocene and Recent sediments of northern Placentia Bay, Newfoundland. Canadian Journal of Earth Sciences, 13: 1386-1392.

Stoner, A.W., and Abookire, A.A. 2002. Sediment preferences and size-specific distribution of young-of-the-year Pacific halibut in an Alaska nursery. Journal of Fish Biology, 61: 540-559.

Sullivan, P.J. 1991. Stock abundance estimation using depth-dependent trends and spatially correlated variation. Canadian Journal of Fisheries and Aquatic Sciences, 48: 1691-1703.

Swartzman, G., Brodeur, R., Napp, J., Hunt, G., Demer, D., and Hewitt, R. 1999. Spatial proximity of age-0 walleye pollock (*Theragra chalcogramma*) to zooplankton near the Pribilof Islands, Bering Sea, Alaska. ICES Journal of Marine Science, 56: 545-560.

Vignaux, M. 1996. Analysis of spatial structure in fish distribution using commercial catch and effort data from the New Zealand hoki fishery. Canadian Journal of Fisheries and Aquatic Sciences, 53: 963-973.

Vilhjálmsson, H. 2002. Capelin (*Mallotus villosus*) in the Iceland-East Greenland-Jan Mayen ecosystem. ICES Journal of Marine Science, 59: 870-883.

Vining, I., Blau, S.F., and Pengilly, D. 2001. Evaluating changes in spatial distribution of blue king crab near St. Matthew Island. *In* Kruse, G.H., Bez, N., Booth, A., Dorn, M.W., Hills, S., Lipcius, R.N., Pelletier, D., Roy, C., Smith, S.J., and Witherells, D. (eds),

Spatial processes and management of marine populations. Lowell Wakefield Fisheries Symposium Series, 17: 327-348.

Welsh, D.W., and Ishida, Y. 1993. On the statistical distribution of salmon in the sea: Application of the negative binomial distribution, and the influence of sampling effort. Canadian Journal of Fisheries and Aquatic Sciences, 50: 1029-1038.

Willey, J.D. 1976. Geochemistry and environmental implications of the superficial sediments in northern Placentia Bay, Newfoundland. Canadian Journal of Earth Sciences, 13:1393-1410.

Williamson, N. J., and Traynor, J.J. 1996. Application of a one-dimensional geostatistical procedure to fisheries acoustic surveys of Alaskan pollock. ICES Journal of Marine Science, 53: 423-428.

4.8 Tables

Table 4.1 The dates, number of blocks, fishing sets and fish sampled per stratum (inner and outer bay) during acoustic surveys conducted in Placentia Bay in 1999. Surveys employed a Biosonics DT 4000 echosounder (120 kHz). The study area comprised of 28 blocks of 120 km^2 each.

Date	Inner bay			Outer bay		
	No. Blocks	No. sets	No. fish	No. Blocks	No. sets	No. fish
7-22 Apr	6	7	251	5	5	122
4-22 May	8	6	78	15	3	39
15-27 Jul	8	6	77	18	9	143
23-30 Oct	8	2	61	12	1	73
2-30 Nov	8	10	149	16	5	97

Table 4.2. Geostatistical fish density indices and coefficient of variation (CV) estimated for the inner bay (I) and outer bay (O) based on acoustic surveys conducted in Placentia Bay during 1999.

Survey month	Stratum	Index (fish.m^{-2})	CV (%)
Apr	I	0.003	10
	O	0.001	13
May	I	0.008	17
	O	0.001	19
Jul	I	0.015	5
	O	0.003	8
Oct	I	0.001	19
	O	0.002	13
Nov	I	0.004	17
	O	0.001	14

4.9 Figures

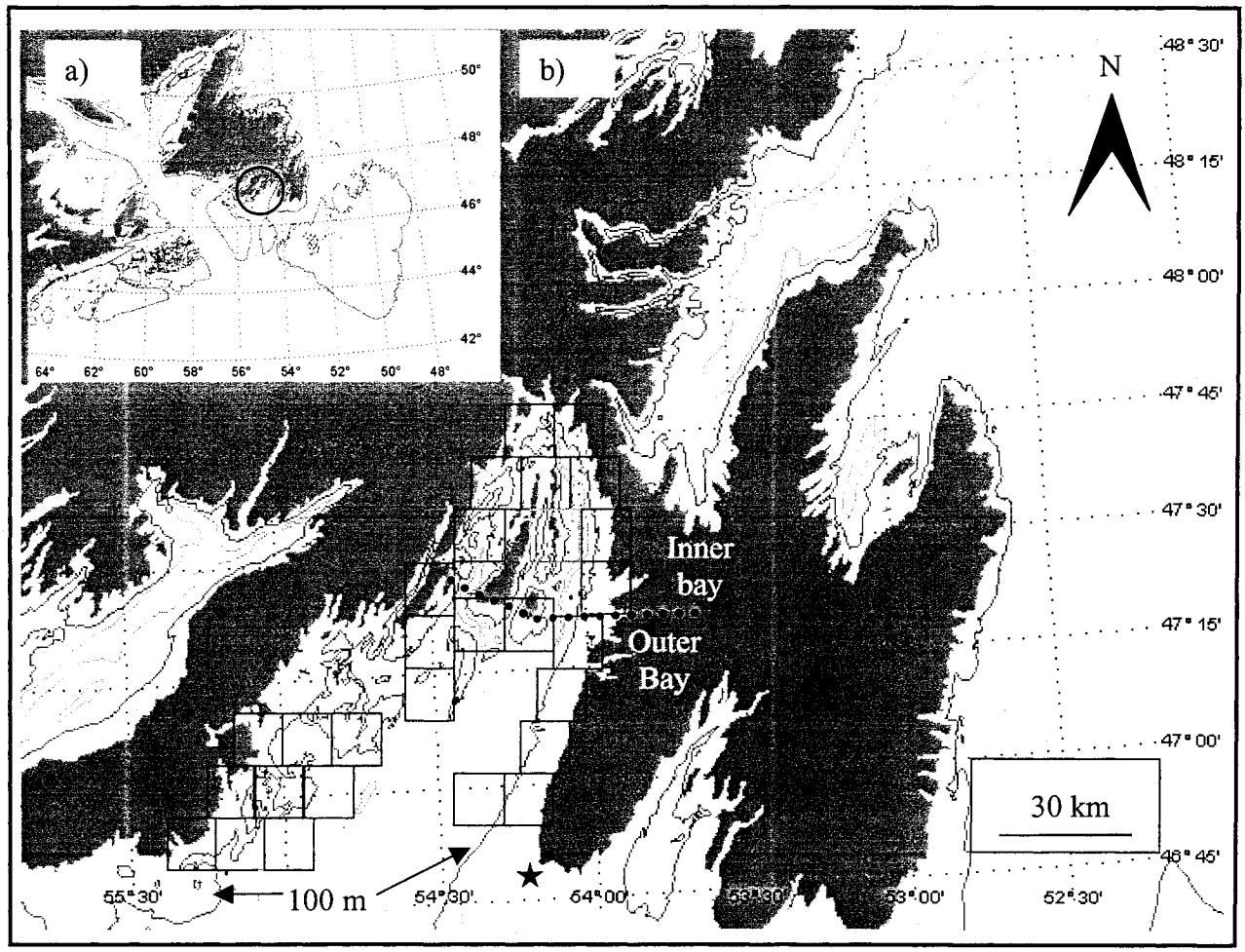


Figure 4.1 (a) East coast of North America showing Placentia Bay (inside circle) on the south coast of Newfoundland and (b) detailed view of the bay showing 100-m depth contour (indicated by black arrow) which represents the limit of acoustic sampling. Dotted line across the bay indicates the division between the inner and outer bay. ★= Cape St. Mary's. Grey squares represent sampling unit areas (1 square = 120 km^2).

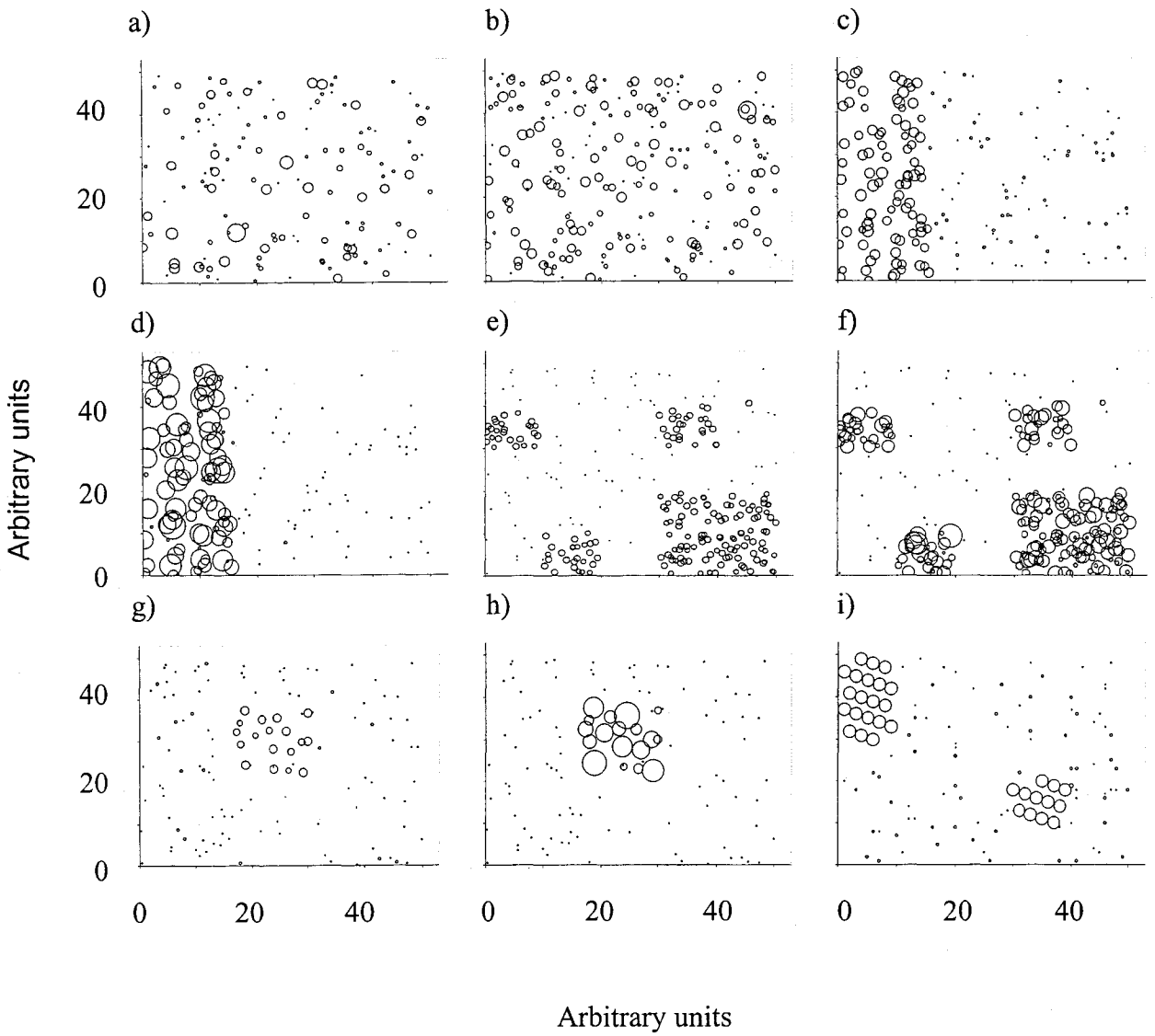


Figure 4.2 Spatial patterns of simulated data according to (a-b) random and (c-i) gregarious distributions.

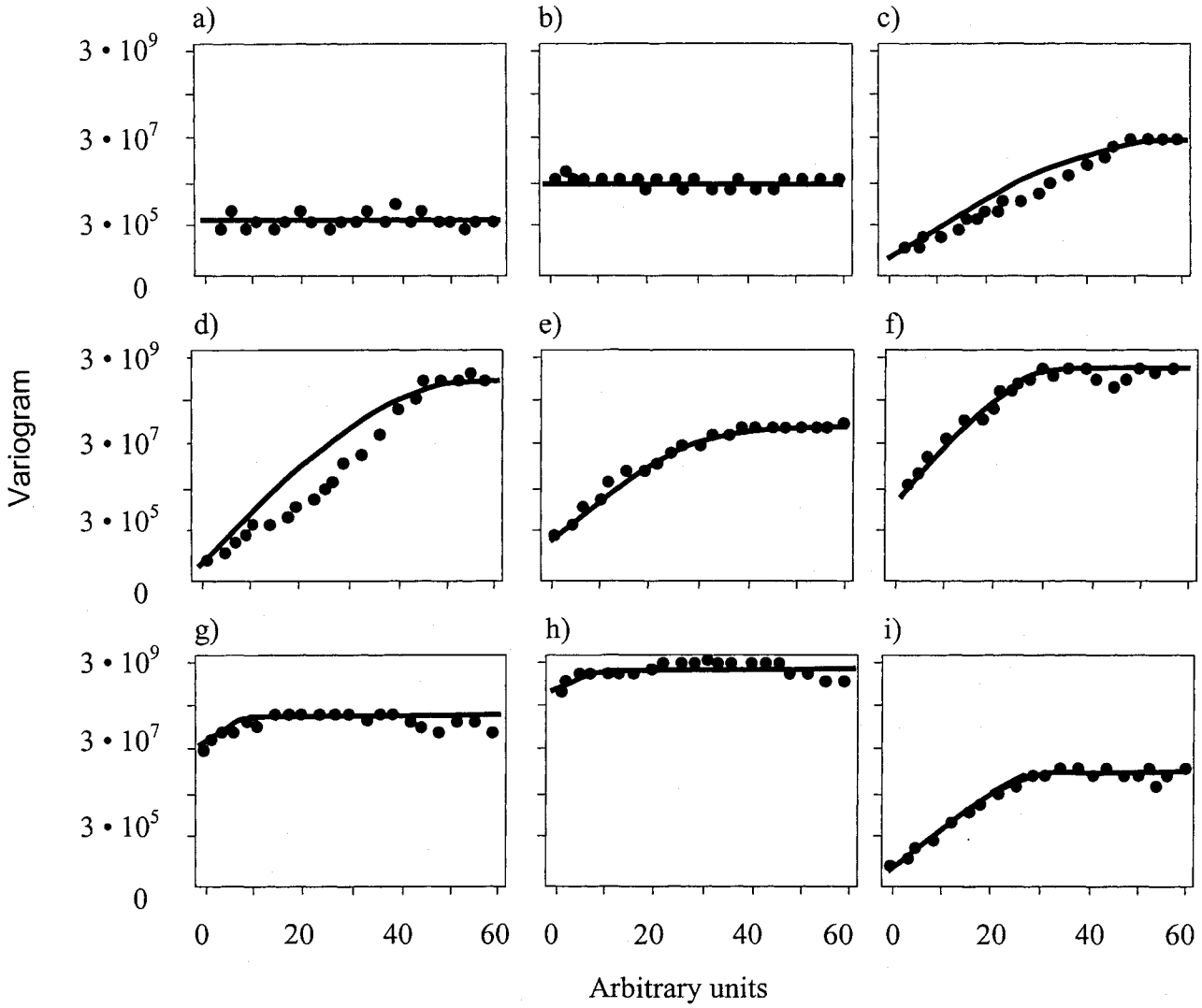


Figure 4.3 Empirical (dot) and theoretical (line) variogram models computed from simulated data according to (a-b) random and (c-i) gregarious distribution patterns. The minimum number of pairs used to compute lag distances (h) was 30.

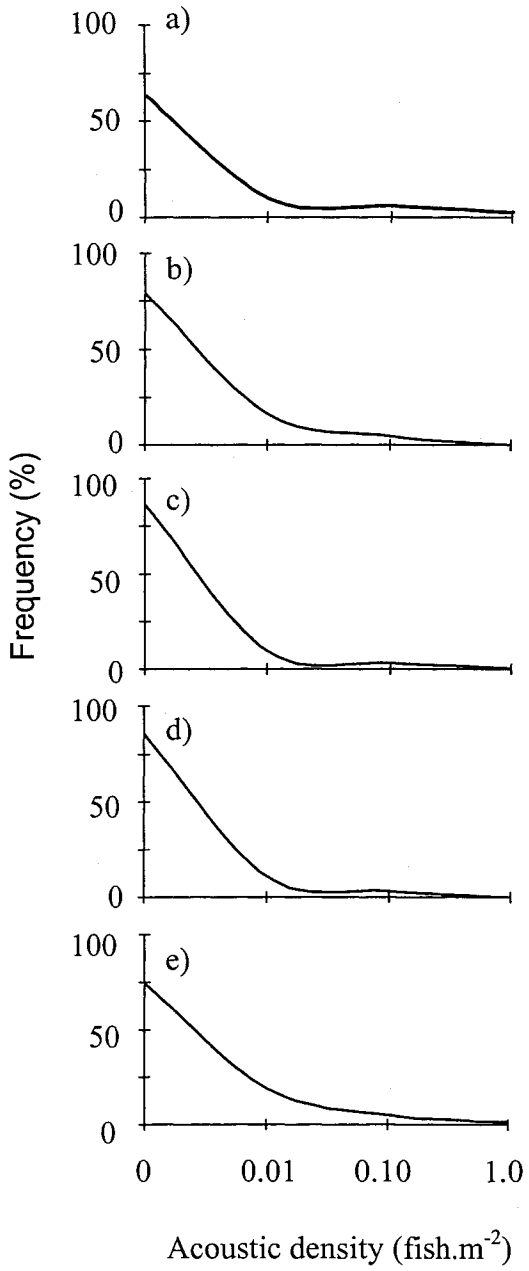


Figure 4.4. Frequency distribution of acoustic density data (fish.m^{-2}) for Placentia Bay cod in (a) April, (b) May, (c) July, (d) October and (e) November 1999.

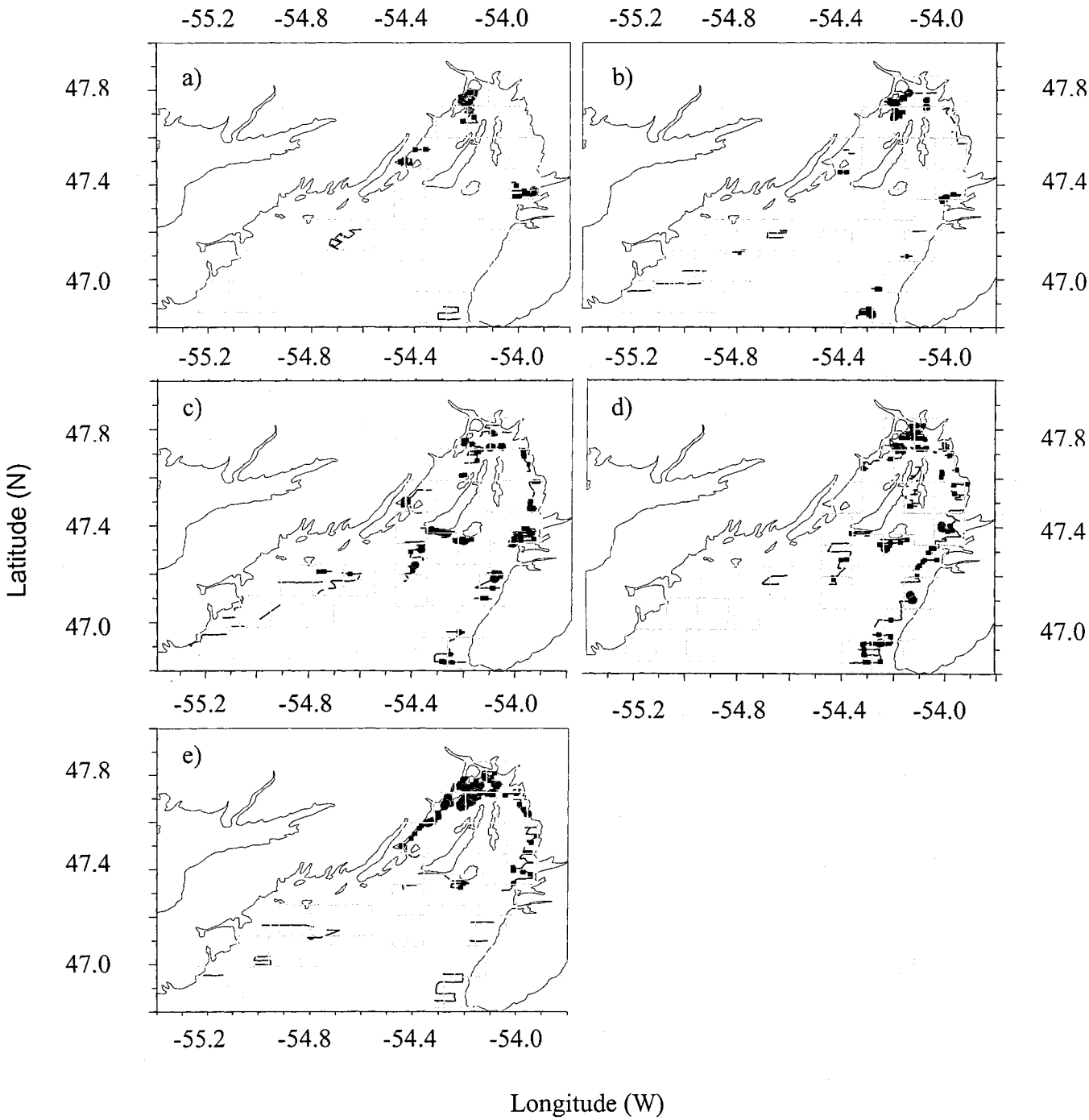
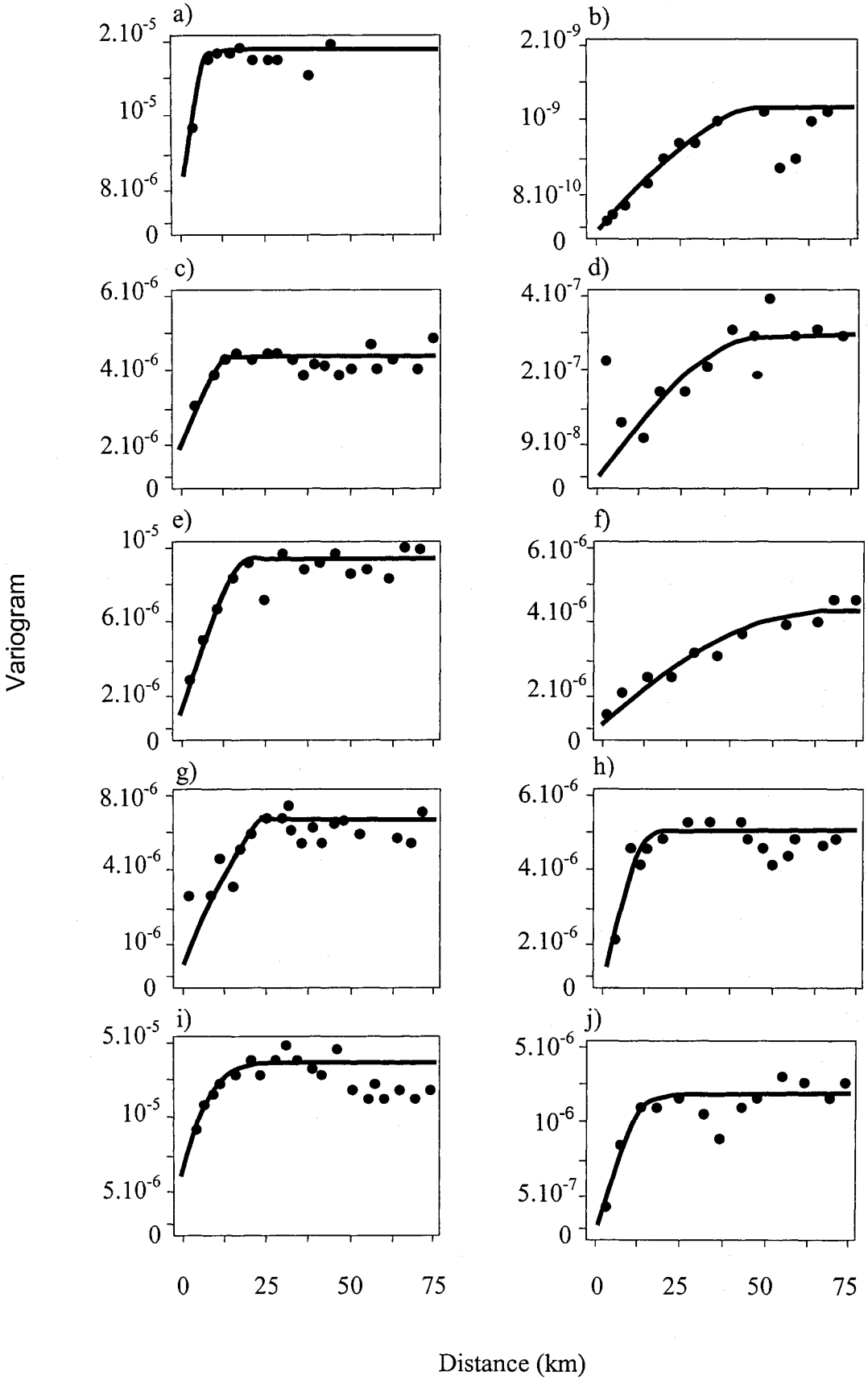


Figure 4.5 Transect track and cod density distribution estimated from acoustic surveys in (a) April, (b) May, (c) July, (d) October and (e) November 1999 in Placentia Bay. Fish density: dotted line (< 0.01 fish.m^{-2}), square (≥ 0.01 and < 0.1 fish.m^{-2}) and circle (≥ 0.1 fish.m^{-2}). Grey squares represent the sampling unit area (120 km^2).

Figure 4.6. Empirical (dot) and theoretical (line) variogram models computed from fish density data. Inner (left panel) and outer bay (right panel). Survey date: (a, b) April, (c, d) May, (e, f) July, (g, h) October, (i, j) November. The minimum number of pairs used to compute lag distances (h) was 30.


a)
b)
c)
d)
e)
f)
g)
h)
i)
j)
Variogram
Distance (km)

Chapter 5 Seasonal variation in abundance and stock composition of Atlantic cod (*Gadus morhua*) in Placentia Bay, Newfoundland in relation to fisheries

5.1 Abstract

Atlantic cod (*Gadus morhua*) in Placentia Bay, Newfoundland, exhibit marked seasonal variation in abundance, age composition and size distribution as the result of mixing of fish from different populations during the post-spawning period and potentially impacting the exploitation rate of stock subcomponents. In this study, a theory is developed to account for these variations. To test it, surveys of distribution, abundance and biological traits of cod were conducted seasonally from fall 1998 to spring 2000 and commercial fishery data were gathered. For the main year of this study in 1999, acoustic estimates of abundance were 4.5 million fish in April, mostly spawning and older cod (ages 7-9). Abundance increased four fold in July, comprised mostly of smaller and younger cod (ages 4-6). By October abundance decreased (5.6 million fish) as summer migrants left the bay, but increased again in November to 6.5 million. The observed seasonal variability in stock abundance, age, size composition and condition indices (K, HSI and GSI) were consistent with the expectations of the theory. Information on commercial catch rates and landings suggested that resident and non-resident cod were targeted by the fishery in different proportions. Estimated harvest rate reached 33% in November 1999 for resident cod. Results of this study emphasize the need for smaller-scale management strategies that take into consideration seasonal changes in the availability of various stock components.

5.2 Introduction

Atlantic cod (*Gadus morhua*) in Placentia Bay, Newfoundland (Figure 5.1) form part of a stock complex (NAFO subdivision 3Ps) comprised of inshore and offshore populations that intermingle at periods other than spawning (Templeman, 1974 and 1979). This stock complex supports a commercial fishery with current annual quota of 15,000 t (Brattey et al., 2003). It has been observed that intermingling of the stock components extends to Placentia Bay, a main centre of the fishery, mainly in late spring and summer (Templeman, 1979; Davis et al., 1994; Lawson and Rose, 2000a). However, the relative sizes of the populations present in the bay through the year are unknown. Despite concerns about the potential for differential exploitation of the stock subcomponents (FRCC, 2001; DFO, 2003) and in particular of overexploitation of the Placentia Bay fish, there has been little examination of this phenomenon.

Using knowledge acquired in previous studies it is possible to build a theoretical framework for the movements and mixing of cod in Placentia Bay. To begin, there is strong evidence of a local coastal population that spawns in the bay during spring. This stock component spawns most consistently near the head of the bay (Lawson and Rose, 2000b; Robichaud and Rose, 2001; Robichaud and Rose, 2002), but also at times over shoals near Cape St. Mary's and Oderin Bank (Templeman, 1979; Lawson and Rose, 2000b). The distribution of cod eggs, larva and juveniles from the head of the bay and along its western side during and after spawning (Robichaud and Rose, 1999; Bradbury et al., 2000) confirms the existence of local spawning. After the spawning season resident

fish tend to move southward along the eastern side of the bay and at times may migrate out of the bay and along the Avalon shore as far as Conception and Trinity Bays (northeast coast). These fish move back into the bay during fall (Brattey et al., 1999a; Lawson and Rose, 2000a). Lawson and Rose (2000a) indicated that most long-distance migratory cod from the local population were larger fish and that smaller fish may stay in the bay throughout the year. By the end of fall cod are found mainly in dense aggregations at the head and western side of the inner bay (Mello and Rose, 2005a) where it is believed that part of the local population overwinter (Davis et al., 1994; Rose, unpublished).

In addition to the resident population, there is also evidence of fish from adjacent coastal and offshore populations visiting Placentia Bay seasonally. Tagging studies conducted in the bay (Lawson et al., 1998; Brattey et al., 1999a) and information from the inshore fishery (Davis et al., 1994; Davis and Jarvis, 1996) indicated that migrant cod are mostly from the St. Pierre Bank, as well as cod moving eastward from Fortune Bay during late spring and summer and returning in the fall. Grand Bank cod may also at times move into Placentia Bay from around Cape St. Mary's during summer. Similar seasonal mixing of stock components has been observed in other regions of the Labrador and Newfoundland shelves (Templeman, 1979).

Historically, the cod fishery in Placentia Bay was prosecuted near year round by a variety of gears including handline, line trawl, otter trawl, trap and gillnet (Davis et al., 1994). In recent years between 30-50% of the total reported catch for 3Ps has been taken in

Placentia Bay (Brattey et al., 2003). Given the likelihood that the bay contains seasonally changing mixes of fish, the timing and location of fishing effort may result in differential exploitation of some stock components (DFO, 2002).

Cod from different geographic areas might be expected to exhibit variation in biological characteristics, because traits such as growth, spawning and fish condition are largely a function of thermal and feeding regimes (Brander, 1995; Schwalme and Chouinard, 1999; Mello and Rose 2005b). Hence, differences in biological traits might hold the potential to identify sub-stocks or stock components of cod (Salvanes et al., 2004). Consequently if the proposed stock mixing theory is correct, it might be expected that the abundance and biological traits of cod in the bay would vary seasonally. In particular less variability in biological traits and abundance would be expected at times of the year when the resident population dominated and the greatest diversity would be expected when both resident and non-resident components were present. In keeping with the proposed mixing, it is anticipated that the proportion of spawning fish should be highest in spring, before the inward-outward migrations of the various stock components occur. It is also expected that the distribution and catch rates of the fishery will parallel the proposed movement and abundance patterns of the stock components.

The purpose of this study is to examine the proposed theory of cod stock structure and movements in Placentia Bay by using biological data and abundance estimates from acoustic surveys and commercial fishery data to test several of its predictions. I then attempt to derive abundance estimates of putative groups of fish during different seasons,

relate these to distribution and movement patterns in the bay and to reproduction and feeding. Finally, I examine potential harvest rates of the identified groups during the 1999 fishery.

5.3 Material and Methods

5.3.1 Acoustic surveys

Placentia Bay is the largest bay in Newfoundland measuring approximately 132 km long with a maximum width of 100 km (Figure 5.1). A total of eight acoustic surveys were conducted in the bay between October 1998 and May 2000 (Table 5.1). Surveys were run over relative short periods of time (8-29 days) providing monthly estimates of abundance and composition and minimizing the effects of intra-seasonal variability caused by changes in fish distribution and movement. The surveys employed a BioSonics DT 4000 echosounder with a 120 kHz transducer mounted on a towed body. The system was calibrated in situ with a tungsten-carbide standard target (Foote et al., 1987).

Previous studies based on seasonal acoustic surveys (Lawson and Rose, 2000a) had shown that from spring to fall cod in Placentia Bay are not commonly found at depths greater then 100 m. Consequently acoustic surveys focused on shallower areas (< 120 m). Because of differences in bathymetric/topographic features within the bay, the study area was divided into two strata, the high relief inner bay and the more homogeneous outer bay. Surveys were conducted over a base grid work of 9 inner bay blocks and 18 outer

bay blocks. Block dimensions were 11 x 11 km and for each block, approximately 11 km of acoustic transects were run during daytime period only along lines of latitude (E-W) with start position randomly selected. The number of transects required to make up the 11 km depended on the topographic and bathymetric features of the area surveyed and navigational obstacles, resulting in many cases of a series of short transects. The order in which blocks were surveyed varied among surveys, depending on weather conditions. In areas with high cod densities (0.1-1 fish.m^{-2}), this standard coverage was then followed by a more intense acoustic sampling (approximately 0.5 km equally spaced parallel transects). Most blocks in each stratum were covered during surveys, except during April 1999 in the outer bay (Table 5.1). In addition, the outer bay was not acoustically surveyed during October-November 1998 and May 2000 and only biological samples are available during these periods.

5.3.2 Biological data

Cod were caught by handline from acoustically identified aggregations during all surveys. Handlining was conducted for 30 minutes using four lines each having six equal sized unbaited hooks (10.2 cm long by 2.6 cm wide). For most surveys, fishing sets were conducted in both the inner and outer bay (Table 5.1). The small number of samples (< 20) of younger and older fish (ages 3 and 10+ respectively) limited analyses to cod ages 4-9. A total of 1716 fish were sampled for total length, total weight, somatic weight (total weight – organ weight), gonad weight, sex and otoliths for age determination. Cod length and weight were measured to the nearest cm and g, respectively. All biological traits

(e.g., age, length and maturity stage distributions, mean weight at age) were calculated using catch from all fishing sets pooled by survey and stratum.

Spawning condition was based on visual classification criteria described in Morrison (1990). Maturity stage was classified in 4 categories: immature, pre-spawning, spawning, and spent. The gonads of immature male and female cod displayed small, translucent, white or pink-like coloration with no blood vessels visible. Pre-spawning female cod had white eggs present in the ovaries and visible at naked eye and males had enlarged pink to white gonads with little or no sperm visible in the efferent ducts. Spawning females had hydrated (translucent) eggs in the ovary and spawning males distended, opaque to white gonads with running milt observed in most cases. Spent female and male had shrunken and soft gonads of pink, grey or white-like coloration.

5.3.3 Identifying putative stock components

Cluster analysis was performed for each combination of survey, stratum and age group (4-9) to identify groups of cod having similar biological traits and to obtain the proportion of fish identified in each group. The traits (components) used in the analysis included somatic weight, gonado-somatic index (GSI = gonad weight/somatic weight), Fulton's K condition factor (K = somatic weight/length^3) and hepato-somatic index (HSI = liver weight/somatic weight) of each fish sampled during acoustic surveys. These variables have been shown to vary seasonally for cod in Placentia Bay (Mello and Rose, 2005b and 2005c) and in other regions (Schwalme and Chouinard, 1999; Yaragina and

Marshall, 2000) and are used in this study as classification or hierarchical criteria to separate groups of cod in Placentia Bay. The unweighted pair-group centroid method (Sneath and Sokal, 1973) was used to determine the distance (dissimilarity level) between two clusters. This method was used because it is more robust to outliers than most other hierarchical methods (SAS, 1990) and no a priori assumptions are necessary (Paukert and Wittig, 2002). Distance was measured as the squared distance between two cluster centroids (average point in a multidimensional space defined by its dimensions). A dissimilarity level > 50% (i.e., majority of observations) was used as a criterion to determine different clusters of fish. The analysis produces hierarchical clusters of similar observations that can be displayed as a hierarchical tree or dendrogram. Variance matrices of the original variables were generated and used to compute eigenvalues, which are equivalent to the percent of the explained standardised variance (SAS, 1990).

5.3.4 Estimation of abundance

Acoustic data (echograms) were edited manually and integrated using FASIT software (Lefeuvre et al., 2000) to determine an area backscattering coefficient for each 100 m interval along survey transects. Fish density (fish.m^{-2}) was estimated as:

$$fish\ density = s_a . \theta_{bs}^{-1} . D^{-1} \quad (1)$$

where s_a is area backscattering coefficient ($m^2.m^{-2}$), θ_{bs} is the arithmetic mean acoustic backscattering cross section of one fish (e.g., $\theta_{bs} = 10^{\frac{TS}{10}}$) as calculated from the target

strength relationship TS (dB) = 20 log (length(cm)) - 67.5 (Rose, 2003) and D is detectability. Detectability values used had been previously determined in experiments conducted on the same stock (Lawson and Rose, 1999).

For each block, the raw acoustic densities were averaged over each minute of latitude and two minutes of longitude, which at latitude 47° N (study area) is roughly equivalent to an area of 3.5 km^2. This procedure standardised sampling effort, while preserving the spatial structure of the data (Mello and Rose, 2005a). Averaging data over regular distance intervals is a common procedure in fisheries acoustics (MacLennan and Simmonds 1992; Rivoirard et al., 2000; Rose, 2003). Acoustic data are recorded continuously along the survey transects and integrated over short distance intervals (in this case for each 100 m), generating very high number of observations.

A fish density index (fish.m^{-2}) was estimated for each stratum and survey using geostatistics (mean and SD). Geostatistical analysis was used because acoustic survey data were in all cases serially correlated as the result of contagious distribution patterns exhibited by cod in Placentia Bay (Mello and Rose, 2005a). The spatial variability of the data was modeled as auto-correlation and incorporated into the estimation procedure by weighting the sample values with the appropriate variogram model (Matheron, 1963). A robust estimator of the variogram (Cressie and Hawkins, 1980) was used:

$$\bar{\gamma}(h) = \frac{\left\{ \frac{1}{2|N(h)|} \sum_{N(h)} |z_i - z_j|^{\frac{1}{2}} \right\}^4}{0.457 + 0.494/|N(h)|} \qquad (2)$$

where N(h) is the set of all pairwise distances i - j = h in a two dimensional plan, |N(h)| is the number of distinct pairs in N(h), z_i and z_j are data values at spatial locations i and j, respectively, 0.457 and 0.494 are model coefficients. The resulting empirical variograms were then fitted with appropriate theoretical variogram models. In all cases, spherical models with or without a nugget term (micro-scale variations of data that are not described by spatial scale) provided the best fit. The model used was:

$$\gamma(h) = c\left[\frac{3|h|}{2a} - \frac{|h|^3}{a^3}\right], \qquad \text{for } |h| < a \tag{3}$$

$$\gamma(h) = c, \qquad \text{for } |h| \geq a \tag{4}$$

where c is the sill of the variogram $\gamma(h)$ representing the maximum level of variability in data measurements, |h| is the scalar distance between two measurements and a is the range of the variogram $\gamma(h)$ and represents the distance at which data are no longer correlated. The nugget model used was:

$$\gamma(h) = 0 \qquad \text{for } h = 0 \tag{5}$$

$$\gamma(h) = c \qquad \text{for } |h| > 0 \tag{6}$$

Ordinary kriging was used to interpolate unsampled locations based on the theoretical variogram weighted by a linear combination of available samples. Kriging predictions were computed as:

$$Z(V) = \sum_{i=1}^{N} \lambda_i Z(x_i) \qquad (7)$$

where Z(V) is the estimate of density at an unsampled point, N is the number of samples, λ_i is the weight attributed to sample x_i. The kriging output included the location (latitude and longitude), fish density predictions (fish.m^{-2}) and the standard deviation of the predictions. The precision of the estimates was obtained by calculating the coefficient of variation (CV). Additional detail on the geostatistical cod density indices is given in Mello and Rose (2005a).

For each survey estimates of the abundance in number were obtained by multiplying the density index by the stratum area (1.2 10^9 m^2 and 2.4 10^9 m^2 for the inner and outer bay, respectively). Estimates of abundance for putative stock components were obtained by multiplying the abundance in number at age by the estimates of the proportion of fish sampled during the surveys having similar biological traits as identified by the cluster analysis. Biomass estimates were obtained by scaling the abundance in number at age by the mean total weight at age (Table 6.1).

5.3.5 Commercial fishery data

Commercial fishery data comprised gear type and daily catch weigh (t) per fisherman obtained from purchase slips made available by National Sea Products (NSP) and monthly catch weight (t) for the commercial cod fishery in Placentia Bay (Brattey *et al.*, 1999b, 2000 and 2001). The catch processed by NSP comprised approximately half of the total commercial catch in the bay during the study period (N. Bolt, NSP, personal communication). Data from NSP were obtained from all regions of the bay (Figure 5.1) and a catch rate index (mean catch weight (t) landed monthly by one fisherman) was calculated for each stratum. Gillnet catch represented up to 95% of the overall catch and therefore no estimates were provided for the remaining gear types used in the fishery (handline, baited trawl and trap). Mesh size (140 mm) of commercial gillnets did not varied seasonally during the study period (Brattey *et al.*, 1999b and 2000) and selected mostly towards fish 60-90 cm in length (Cadigan and Brattey, 2000; Parsons and Stead, 2003).

5.4 Results

5.4.1 Age, length and maturity

The age frequency distribution of survey catch differed significantly among months in both 1998 (inner bay: χ^2= 29.8, df = 6, P < 0.0001) and 1999 (inner bay: χ^2= 89.7, df = 24, P < 0.0001; outer bay: χ^2= 44.1, df = 12, P < 0.0001). In spring (April-May) older

cod could be located in either the inner or outer bay (Figure 5.2). In 1999 57-60% of the fish sampled in the inner bay were aged 7-9 years, but only 24% where of these ages in May 2000. In the outer bay older cod comprised between 32-54% in 1999 but up to 78% in May 2000. By July younger cod (ages 4-6) dominated the catch in both areas of the bay (59-65%). The proportion of younger cod caught during surveys increased in October in the inner bay (77%) and outer bay (68%) and then declined in November as the proportion of older cod increased up to 30% and 46% in the inner and outer bay, respectively. Similar patterns were observed during the fall 1998, particularly in the inner bay, while in the outer bay no marked change in age composition was observed. In addition, a comparison of the data in 1998 and 1999 indicates that in most cases there were no apparent differences in the younger versus older cod between inner and outer bay either year.

Length frequencies also differed significantly among months in both 1998 (inner bay: $\chi^2 = 55.9$, df = 14, $P < 0.0001$) and 1999 (inner bay: $\chi^2 = 122.3$, df = 52, $P < 0.0001$; outer bay: $\chi^2 = 58.1$, df = 24, $P < 0.0001$). In 1999 survey catches in the inner bay comprised a larger proportion of cod $\geq$ 60 cm in April, May and November when compared with the July and October catches (Figure 5.3). The range of sizes taken in survey catches decreased between May and July in both inner and outer bay, but increased between October and November in both 1998 and 1999. The range and frequency of sizes in the outer bay was in most cases similar to that observed for the inner bay during the same periods, except in October (1998-1999) and November (1999) when fish $\geq$ 64 cm comprised a larger proportion of the catch than in the inner bay.

Cod in pre-spawning and spawning condition were observed mainly during April-July (43-80% of survey catches) in the inner bay and April-May (44-73% of survey catches) in the outer bay (Figure 5.4). The proportion of spent cod increased during July (27-49%) and peaked in the fall (up to 83%) in both strata.

5.4.2 Distribution

Cod density estimates were not available for the outer bay in October-November 1998 and May 2000, as only the inner bay was acoustically surveyed during these periods. The 1998 data were uncalibrated as a consequence of an equipment failure and are presented only to compare distribution patterns between 1998-1999.

Most cod were found in a few large aggregations with relatively high densities in the eastern side of the inner bay in October 1998 and at the head of the bay in November (Figure 5.5). A similar patchy distribution was again observed in April-May 1999 in the inner bay, whereas the outer bay had widely scattered and low fish densities (< 0.01 fish.m^{-2}), with the exception of a high density aggregation near Cape St. Mary's in May. In May 2000, densities were lower but similarly distributed throughout the inner bay. By July, cod were more dispersed and found in many areas of the bay in small dense aggregations ($\geq$0.1 fish.m^{-2}). A similar distribution pattern predominated in October although fewer fish were located over the banks of the outer bay. In November, most cod were located at the head of the bay in moderate to high density aggregations in 1998-1999.

5.4.3 Weight and condition

Mean somatic weight, K and HSI tended to be lowest during the spawning season (spring) and increased rapidly during the post-spawning period, reaching maximum values by fall (see Fig. 2 in Mello and Rose, 2005c). GSI peaked in April for age 4 and 9 and during May-June for ages 6-8. Minimum values occurred in January for cod age 4 and July-October for ages 5-9 (see Table 5 in Mello and Rose, 2005b).

Cluster analysis was performed where sample number permitted. In cases where sample sizes were low ($n < 20$) cluster analysis results should be interpreted with caution. Most dendrograms where of two types (Figure 5.6). The first had few or no clusters at dissimilarity level > 50%. This type of dendrogram was mostly observed in April (1999) and October (1998-1999) in both strata and May (1999-2000) in the outer bay (Table 5.2). The second dendrogram had 2-3 large clusters and was observed mainly in the inner bay in November 1998 and May (1999-2000) and in both areas of the bay in July and November 1999. Dendrograms containing more than one cluster were most frequent in ages 5-7, particularly in July and November 1999. The proportion of fish identified in cluster 1 varied among dendrograms between 41-100%, while cluster 2 accounted for 11-50% and up to 21% of the cod ages 5 and 7 sampled in the outer bay in July were identified in a third cluster.

In most cases all variables contributed to cluster formation as indicated by the relative high percentage of the variance explained by each component. Components one and two accounted for 30-88% and 10-39% of the variability in the data, respectively, whereas the

inclusion of a third and fourth components explained an additional 3-23% and 3-20% of the variance (Figure 5.7). The analysis for the outer bay produced similar results, with 1 to 4 components accounting for 30-72%, 19-41%, 3-28% and 2-21% of the variance, respectively.

5.4.4 Geostatistical analysis of fish density and estimation of abundance

Overall there was a good fit of theoretical to empirical variograms and low level of unexplained variability, as most variograms had small nugget effects. Variogram range varied 9-67 km and was higher in the outer bay in all months except October (see Fig. 6 in Mello and Rose, 2005a). Variogram sill varied between 10^{-9} and 3.10^{-6} $(fish.m^{-2})^2$ and was lower in the outer bay in all months. Nugget effect was observed in several variograms. Large nugget effect occurred in the inner bay in April, May and November (20-27% of the sill). However, in most cases nugget effect was low (< 8 % of the sill).

During 1999 density indices increased from April to July in the inner bay from 0.003 to 0.01 $fish.m^{-2}$ and from 0.001 to 0.003 $fish.m^{-2}$ in the outer bay (Table 5.3). Density indices decreased between July and October, particularly in the inner bay, to 0.001 $fish.m^{-2}$ and then increased in November to 0.004 $fish.m^{-2}$. Overall, density indices were higher in the inner bay in all periods except in October. The density index was 4-fold smaller in May 2000 than in May 1999. CVs varied between 5% (July) and 19% (May and October).

In 1999, abundance was lowest in April (4.5 million fish and 10,000 t) with most fish found in the inner bay (Table 5.3). Estimates increased through May (11.1 million fish and 27,900 t) with most fish still located in the inner bay and peaked in July (17.8 million fish and 35,600 t) when a considerable portion of the stock (38%) was found scattered through the outer bay. Abundance declined between the July and October, to 5.6 million fish (14,000 t) with most fish found in the outer bay (70%). In November, abundance increased to 6.5 million fish (15,300 t) with most fish (72%) located in the inner bay. Estimated abundance was much lower (2 million fish and 4,100 t) in May 2000 than in spring of 1999 in the inner bay. The number of fish identified in cluster 1 ranged from 0.1 million fish (200 t) in April (outer bay) up to a maximum of 9.4 million fish (17,900 t) in July (inner bay), whereas clusters 2 and 3 contained 0.2-1.6 million fish (200-3,600 t) and 0.5 million fish (1,100 t), respectively (Table 5.3).

5.4.5 Commercial catch

Monthly catch rates from NSP fishers corresponded well to monthly catch landings for the fishery in Placentia Bay (Figure 5.8). Catch patterns indicated a typically contracted fishery with 71-86% of the annual catches occurring during 4 months over the summer and fall in 1998-1999 and winter, summer and fall in 2000. Practically no commercial fishery (< 5%) occurred during the first half of the year in 1998-1999 and < 30% in 2000 (January-February). Catch rates were higher in the inner bay during most periods and peaked during November in 1998-1999 (5.9-9.1 $t.month^{-1}$) and February in 2000 (3.1-7.1 $t.month^{-1}$).

5.5 Discussion

The results from this study are for the most part consistent with the predictions of the theory of stock structure and mixing advanced here. Large within-year variation in abundance estimates and biological traits of cod sampled in Placentia Bay were observed for the main year of this study (1999), as acoustic estimates of cod abundance in Placentia Bay increased up to 4-fold between spring and summer, followed by a decline through the fall. These changes were accompanied by changes in age composition and length distribution, with a predominance of older (7-9) and larger (> 60 cm) cod during spawning (April-May), younger and smaller cod in summer (July) and early fall (October) and followed by an increase in the proportion of older and larger fish by November. These variations coincide with the expected influx of non-resident fish into the bay during the post-spawning period and moving out again in the fall (Templeman, 1979; Brattey et al., 1999a; Lawson and Rose, 2000a). Stomach content analysis of cod sampled during the surveys indicated intense feeding activity (particularly on capelin, *Mallotus villosus*) during June-July (Mello and Rose, 2005b). This would suggest that the influx of non-resident cod into the bay during this period is related to feeding migrations. Migrating seasonally to feed is a common behaviour among Newfoundland and Labrador cod stocks in inshore and offshore areas (Templeman, 1979; Rose, 1993 and 2003) and from other regions (Brander, 1994; Schwalme and Chouinard, 1999).

Cluster analysis showed that fish in different condition (including reproductive condition) are present in the bay simultaneously and that there is more variability in biological traits

in some areas and periods the year (May, July and November). For example, during 1999 the samples from the April survey exhibited no differences at the 50% dissimilarity level, consistent with the expectation that only the residential population is present in the bay at this time. This is supported by the observation of spawning occurring at the same time (Robichaud and Rose, 2001) and as expected it is the period when the largest proportion of the fish caught were in spawning condition. However, during May and July 2-3 clusters or groups of cod (mostly among ages 5-7) were identified. While such results might have been caused by the increased diversity in spawning or reproductive condition as evident at this time, the increase in clusters is also consistent with an influx and mixing of cod from different populations that have experienced different temperature and feeding conditions (Brander, 1995; Salvanes et al., 2004). This interpretation is supported by an increase in cod abundance and decrease in size and age composition observed at the same time. As theorized, it would appear that these migrant fish from other populations leave the bay in October, as abundance declines again, although age and length frequencies remained truncated. This coincides with the reduction in variability of biological traits of the fish present in either inner or outer bay as only one cluster was identified across age groups. The reappearance of 2 different clusters or groups of cod during November coupled with an increase in abundance and of the proportion of older and larger cod is consistent with an additional influx of fish into the bay during this period. These fish were in top condition indicating they had been feeding actively (Mello and Rose, 2005c) and consequently likely representing the returning summer migrants from the resident population and hence, explaining the apparent inconsistency of high variability in fish condition in November when it is believed that the resident component predominates.

Catch rates of the commercial fishery tended to parallel the distribution and abundance of cod shown in the acoustic surveys. Landings were high in summer when abundance peaked, but catch rates were low. This is consistent with a high abundance but more dispersed fish distribution and perhaps reduced catchability. In contrast, landings and catch rates were both high in the fall and winter, as the result of more aggregated fish distributions, particularly in the inner bay.

When landing patterns of the fishery and biological characteristics of the stock as described previously are considered together, the timing of removals would suggest that resident and non resident fish are being harvested in different proportions. Acoustic estimates of cod biomass during the main fishing periods in 1999 ranged from 35,600 t (July) to 14,000-15,300 t (October-November) and the reported catch weight was 1,850 t and 1,300-5,050 t (Brattey et al., 2000) during the same periods. Assuming that the acoustic estimates provide a comparable index across seasons, the estimated annual harvest rate would range from approximately 5% in July to 9-33% during October-November. As removals were heaviest in the fall (highest catch rates and landings) subsequent to the departure of non-resident fish, it is likely that resident fish were preferentially targeted by the fishery. If one assumes similar temporal patterns in abundance estimates and movement of fish in and out of the bay during 2000, the resident component was then likely heavily targeted by the fishery in that year as well since 28% of the total landings occurred in winter and 40% in fall (Brattey et al., 2001). No acoustic estimates of cod abundance and distribution are available during the winter. However, high catch rates were observed in the inner bay at this time, indicating that a portion of

the population was present in this region of the bay, likely on overwintering grounds when they were harvested.

As many as three distinct groups of fish were identified by the cluster analysis during July. Using the percentage composition of fish identified in each cluster it was estimated that these three clusters were comprised of approximately 18,000 t, 6,700 t and 1,100 t, respectively. Consequently, if the fishery targeted a particular group of fish, harvest rates from the lower abundance clusters (1,100-6,700 t) could potentially be much higher than that estimated for the bay overall. Similarly, the estimated biomass of fish identified in the lower abundance cluster in November (3,000 t) could also result in exploitation higher than the 33% estimated for the stock overall if this group was targeted by the fishery.

It is noted that identification of stock components in the harvest is not possible with the present data, hence differential harvest rates among components must be viewed as possible but not proven. Nevertheless, it is thought that if the theory of stock components movements and abundance is basically correct, as this study suggests, then an even harvest of these components appears unlikely and furthermore, that resident Placentia Bay fish are very likely to have been harvested at a much higher rate than the other stock components.

Gear selectivity may also have influenced the results of this study, but only in a minor way. Cod were caught during surveys primarily using handlines. Although the fishery

largely used gillnet (83-95% of the total catch weight during the study period), it is not expected these gear differences to be a point of concern in most cases. Both gears have similar selectivity for fish 60-80 cm (Cadigan and Brattey, 2000), which comprises the range of sizes of most cod caught in Placentia Bay during surveys and by commercial gillneters (Parsons and Stead, 2003). Selectivity may be an issue with smaller fish as handlining has a higher selectivity for fish < 55 cm (total length) than does gillnetting (Cadigan and Brattey, 2000). Discarding of cod in the commercial fishery may also result in an underestimation of exploitation rates. Discarding might be particularly important at times when the fishery is likely to harvest a higher proportion of younger fish (e.g., July or October).

In summary, this study shows that the cod stock in Placentia Bay experiences marked variations in abundance and composition over the annual cycle. These variations appear to be related to movement and mixing of fish from different populations and that the observed variability impacted the commercial fishery (catch rates and landings). The findings largely support the theoretical framework of stock movement and mixing based on previous studies. The present study suggests that current harvesting strategies have high potential to differentially exploit the various stock components with the heaviest exploitation of the resident stock in Placentia Bay (at least in 1999). The findings of this study emphasise the need for the development of smaller-scale (e.g., bay scale, stock component scale) management strategies (Frank and Brickman, 2000), and take into consideration seasonal changes in the availability of various stock components.

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5.7 References

Bradbury, I.R., Snelgrove, P.V.R., and Fraser, S. 2000. Transport and development of eggs and larvae of Atlantic cod, *Gadus morhua*, in relation to spawning time and location in coastal Newfoundland. Canadian Journal of Fisheries and Aquatic Sciences, 57: 1761-1772.

Brander, K.M. 1995. The effect of temperature on growth of Atlantic cod (*Gadus morhua* L.). ICES Journal of Marine Science, 52: 1-10.

Brander, K.M. 1994. Spawning and life history information for North Atlantic cod stocks. ICES Cooperative Research Report 205.

Brattey, J., Cadigan, N.G., Healey, B.P., Lilly, G.R., Murphy, E.F., Stansbury, D.E., and Mahé, J.-C. 2003. An assessment of the cod (*Gadus morhua*) stock in NAFO Subdivision 3Ps in October 2003. DFO Canadian Science Advisory Secretariat Research Document 2003/092.

Brattey, J., Cadigan, N.G., Healey, B.P., Lilly, G.R., Murphy, E.F., Shelton, P.A., Stansbury, D.E., Morgan, M.J., and Mahé, J.-C. 2001. An assessment of the cod (*Gadus morhua*) stock in NAFO Subdivision 3Ps in October 2001. DFO Canadian Science Advisory Secretariat Research Document 2001/99.

Brattey, J., Cadigan, N.G., Lilly, G.R., Murphy, E.F., Shelton, P.A., and Stansbury, D.E. 2000. An assessment of the cod stock in NAFO Subdivision 3Ps in October 2000. DFO Canadian Science Advisory Secretariat Research Document 2000/134.

Brattey, J., Lawson, G.L., and Rose, G.A. 1999a. Seasonal migration patterns of Atlantic cod (*Gadus morhua*) in NAFO subdivision 3Ps based on tagging experiments during 1997-98. DFO Canadian Science Advisory Secretariat Research Document 99/37.

Brattey, J., Cadigan, N.G., Lilly, G.R., Murphy, E.F., Shelton, P.A., and Stansbury, D.E. 1999b. An assessment of the cod (*Gadus morhua*) stock in NAFO Subdivision 3Ps. DFO Canadian Science Advisory Secretariat Research Document 99/36.

Cadigan, N., and Brattey, J. 2000. Lower bounds on the exploitation of cod (*Gadus morhua*) in NAFO Divisions 3KL and Subdivision 3Ps during 1997-1999 from tagging experiments. DFO Canadian Stock Assessment Secretariat Research Document 2000/73.

Cressie, N., and Hawkins, D.M. 1980. Robust estimation of the variogram. Mathematical Geology, 12: 115-125.

Davis, M. B. and H. Jarvis 1996. Results from the 1995 inshore Sentinel survey for cod in NAFO Subdivision 3Ps. DFO Atlantic Fisheries Research Document 96/95.

Davis, M.B., Lundrigan P., and Ripley, R. 1994. A description of cod stock structure in Placentia Bay, NAFO Subdivision 3Ps. DFO Atlantic Fisheries Research Document 94/32

DFO, 2003. Subdivision 3Ps cod. DFO Stock Status Report 2003/043.

DFO, 2002. Subdivision 3Ps cod. DFO Stock Status Report A2-02 (2002).

DFO, 2000. Subdivision 3Ps cod. DFO Stock Status Report A2-02 (2000).

Frank, T. K., and Brickman, D. 2000. Allee effects and compensatory population dynamics within a stock complex. Canadian Journal of Fisheries and Aquatic Sciences, 57: 513-517.

FRCC (Fisheries Resource Conservation Council), 2001. 2001 Conservation requirements for groundfish stocks in Sub-areas 0, 2+3. Report to the Minister of Fisheries and Oceans, FRCC. 2001, R.2, March 2001.

Foote, K.G., Knudsen, H.P., and Vestnes, G. 1987. Calibration of acoustic instruments for fish density estimation: a practical guide. ICES Cooperative Research Report 144.

Lawson, G.L., and Rose, G.A. 2000a. Seasonal distribution and movements of coastal cod (*Gadus morhua*) in Placentia Bay, Newfoundland. Fisheries Research, 49: 61-75.

Lawson, G.L., and Rose, G.A. 2000b. Small-scale spatial and temporal patterns in spawning of Atlantic cod (*Gadus morhua*) in coastal Newfoundland waters. Canadian Journal of Fisheries and Aquatic Sciences, 57: 1011-1024.

Lawson, G.L., and Rose, G.A. 1999. The importance of detectability to acoustic surveys of semi-demersal fish. ICES Journal of Marine Science, 56: 370-380.

Lawson, G. L., Rose, G. A., and Brattey, J. 1998. Movement patterns of inshore cod in Subdivision 3Ps (southern Newfoundland) based on marked-recapture studies during 1996-97. DFO Canadian Stock Assessment Research Document 24.

Lefeuvre, P., Rose, G.A., Gosine, R., Hale, R., Pearson, W., and Khan, R. 2000. Acoustic species identification in the Northwest Atlantic using digital image processing. Fisheries Research, 47: 137-147.

Matheron, G. 1963. Principles of geostatistics. Economic Geology, 58: 1246-1266.

MacLennan, D.N., and Simmonds, E.J. 1992. Fisheries acoustics. Chapman and Hall, London.

Mello, L.G.S., and Rose, G.A. 2005a. Using geostatistics to quantify seasonal distribution and aggregation patterns of fishes: an example of Atlantic cod (*Gadus morhua*). Canadian Journal of Fisheries and Aquatic Sciences, 62: 659-670.

Mello, L.G.S., and Rose, G.A. 2005b. Seasonal growth of Atlantic cod (*Gadus morhua* L.): effects of temperature, feeding and reproduction. Journal of Fish Biology, 67: 149-170.

Mello, L.G.S, and Rose, G.A. 2005c. Seasonal cycles in weight and condition in Atlantic cod (*Gadus morhua* L) in relation to fisheries. ICES Journal of Marine Science, 62: 1006-1015.

Morrison, C.M. 1990. Histology of the Atlantic cod, *Gadus morhua*: an atlas. Reproductive tract. Canadian Special Publication in Fisheries and Aquatic Sciences 110.

Parsons, D.M., and Stead, R. 2003. Sentinel surveys 1995-2002: Catch per unit effort in NAFO Subdivision 3Ps. Canadian Science Advisory Secretariat Research Document 2003/021.

Paukert, C.P., and Wittig, T.A. 2002. Applications of multivariate statistical methods in fisheries. Fisheries Research, 9: 16-22.

Rivoirard, J., Simmonds, J., Foote, K.G., Fernandes, P., and Bez, N. 2000. Geostatistics for estimating fish abundance. Blackwell Science, Cornwall.

Robichaud, D., and Rose, G.A. 2002. Assessing evacuation rates and spawning abundance of marine fishes using coupled telemetric and acoustic surveys. ICES Journal of Marine Science, 59: 254-260.

Robichaud, D., and Rose, G.A. 2001. Multiyear homing of Atlantic cod to a spawning ground. Canadian Journal of Fisheries and Aquatic Science, 58: 2325-2329.

Robichaud, D., and Rose, G.A. 1999. Distribution of 0 and 1 group cod in nearshore waters of Placentia Bay (NAFO sub-division 3Ps), 1997-1998. NAFO SCR 99/66.

Rose, G.A. 2003. Monitoring coastal northern cod: towards an optimal survey of Smith Sound, Newfoundland. ICES Journal of Marine Science, 60: 453-462.

Rose, G.A. 1993. Cod spawning on a migration highway in the North-west Atlantic. Nature, 366: 458-461.

Salvanes, A.G.V., Skjæraasen, J.E., and Nilsen, T. 2004. Sub-populations of coastal cod with different behaviour and life-history strategies. Marine Ecology Progress Series, 267: 241-251.

SAS. 1990. SAS/STAT User's guide, version 6, fourth edition, volume 1. Cary, NC: SAS Institute Inc., 1990.

Schwalme, K., and Chouinard, G.A. 1999. Seasonal dynamics in feeding, organ weights, and reproductive maturation of Atlantic cod (*Gadus morhua*) in the southern Gulf of St. Lawrence. ICES Journal of Marine Science, 56: 303-319.

Sneath, P.H.A., and Sokal, R.R. 1973. Numerical taxonomy, the principles and practice of numerical classification. Freeman, San Francisco.

Templeman, W. 1979. Migration and intermingling of stocks of Atlantic cod, *Gadus morhua*, of the Newfoundland and adjacent areas from tagging in 1962-66. ICNAF Research Bulletin, 14: 5-50.

Templeman, W. 1974. Migrations and intermingling of Atlantic cod (*Gadus morhua*) stocks of the Newfoundland area. Journal of Fisheries Research Board of Canada, 6: 1073-1092.

Yaragina, N.A., and Marshall, C.T. 2000. Tropic influences on interannual and seasonal variation in the liver condition index of Northeast Arctic cod (*Gadus morhua*). ICES Journal of Marine Science, 57: 42.55.

5.8 Tables

Table 5.1 The dates, number of blocks, fishing sets and fish sampled per stratum (inner and outer bay) during acoustic surveys conducted in Placentia Bay (1998-2000). Surveys employed a Biosonics DT 4000 echosounder (120 kHz).

Date		Inner bay		Outer bay	
Year	Month	No. sets	No. fish	No. sets	No. fish
1998	Oct	8	106	3	64
	Nov	26	243	4	107
1999	Apr	7	251	5	122
	May	6	78	3	39
	Jul	6	77	9	143
	Oct	2	61	1	73
	Nov	10	149	5	97
2000	May	8	71	7	35
	Total	73	1036	37	680

Table 5.2 Results of the cluster analysis of biological traits of cod ages 4-9 sampled during acoustic surveys in Placentia Bay comprised of the percentage (%) of fish identified in 1-3 cluster centroids (C1-C3) as displayed by each dendrogram and n = number of fish used in each cluster analysis.

Year	Month	Age	Inner bay				Outer bay			
			n	C1	C2	C3	n	C1	C2	C3
1998	Oct	4	26	100			22	100		
		5	25	100			25	78	22	
		6	27	100			17	100		
		7	22					100		
		8	6					100		
		9								
	Nov	4	39	83	17		21	100		
		5	52	79	21		33	64	36	
		6	61	77	23		31	100		
		7	37	86	14		15	100		
		8	38	72	28		7	100		
		9	16	63	37					
1999	Apr	4	22	100			12	100		
		5	51	100			23	100		
		6	54	100			24	100		
		7	65	100			30	100		
		8	25	100			23	100		
		9	34	100			10	100		
	May	4	4	100						
		5	12	87	13		8	100		
		6	21	84	16		10	100		
		7	26	84	16		21	100		
		8	5	100						
		9	10	79	21					

Table 5.2 (cont.) Results of the cluster analysis of biological traits of cod ages 4-9 sampled during acoustic surveys in Placentia Bay comprised of the percentage (%) of fish identified in 1-3 cluster centroids (C1-C3) as displayed by each dendrogram and n = number of fish used in each cluster analysis.

Year	Month	Age	Inner bay				Outer bay			
			n	C1	C2	C3	n	C1	C2	C3
1999	Jul	4	4	100			21	80	20	
		5	24	100			30	41	38	21
		6	24	63	67		27	80	20	
		7	22	78	22		52	46	35	19
		8	3	100			2	100		
		9					11	50	50	
	Oct	4	7	100			9	100		
		5	24	100			27	100		
		6	22	100			23	100		
		7	4	100			10	100		
		8	4	100			4	100		
		9								
	Nov	4	10	86	14		4	100		
		5	26	83	17		21	54	46	
		6	59	68	32		27	55	45	
		7	21	75	25		28	77	23	
		8	21	58	42		14	100		
		9	12	80	20		3	100		
2000	May	4	15	80	20		3	100		
		5	21	76	24		4	100		
		6	22	87	13		11	100		
		7	3	100			7	100		
		8	5	100			5	100		
		9	5	100			5	100		

Table 5.3 Cod density index, CV (%) and estimates of abundance in number (n x 10^6) and biomass (wt x 10^3 t) for Placentia Bay. Abundance estimate for each cluster (C1-C3) was obtained by multiplying the abundance in number at age by the proportion of fish having similar biological traits as identified in the cluster analysis (Table 5.2). The biomass was obtained by scaling the abundance in number at age by the total weight at age (kg) from cod caught during the surveys. No estimates are available for the outer bay in October and November 1998, as well as May 2000. I = inner bay and O = outer bay.

Survey			Density (CV)	C1		C2		C3		Total	
Year	Month	Stratum	(Fish.m^{-2})	n	wt	n	wt	n	wt	n	wt
1999	Apr	I	0.003 (10)	4.4	9.8					4.4	9.8
		O	0.001 (13)	0.1	0.2					0.1	0.2
	May	I	0.008 (17)	8.3	21.1	1.1	2.6			9.4	23.7
		O	0.001 (19)	1.7	4.3					1.7	4.3
	Jul	I	0.01 (5)	9.4	17.9	1.6	3.6			11.0	21.5
		O	0.003 (8)	4.7	10.1	1.6	3.1	0.5	1.1	6.8	14.3
	Oct	I	0.001 (19)	1.7	4.2					1.7	4.2
		O	0.002 (13)	3.9	9.8					3.9	9.8
	Nov	I	0.004 (17)	3.9	9.1	0.8	1.9			4.7	11.0
		O	0.001 (14)	1.3	3.3	0.5	1.1			1.8	4.4
2000	May	I	0.002 (19)	1.8	3.9	0.2	0.2			2	4.1

5.9 Figures

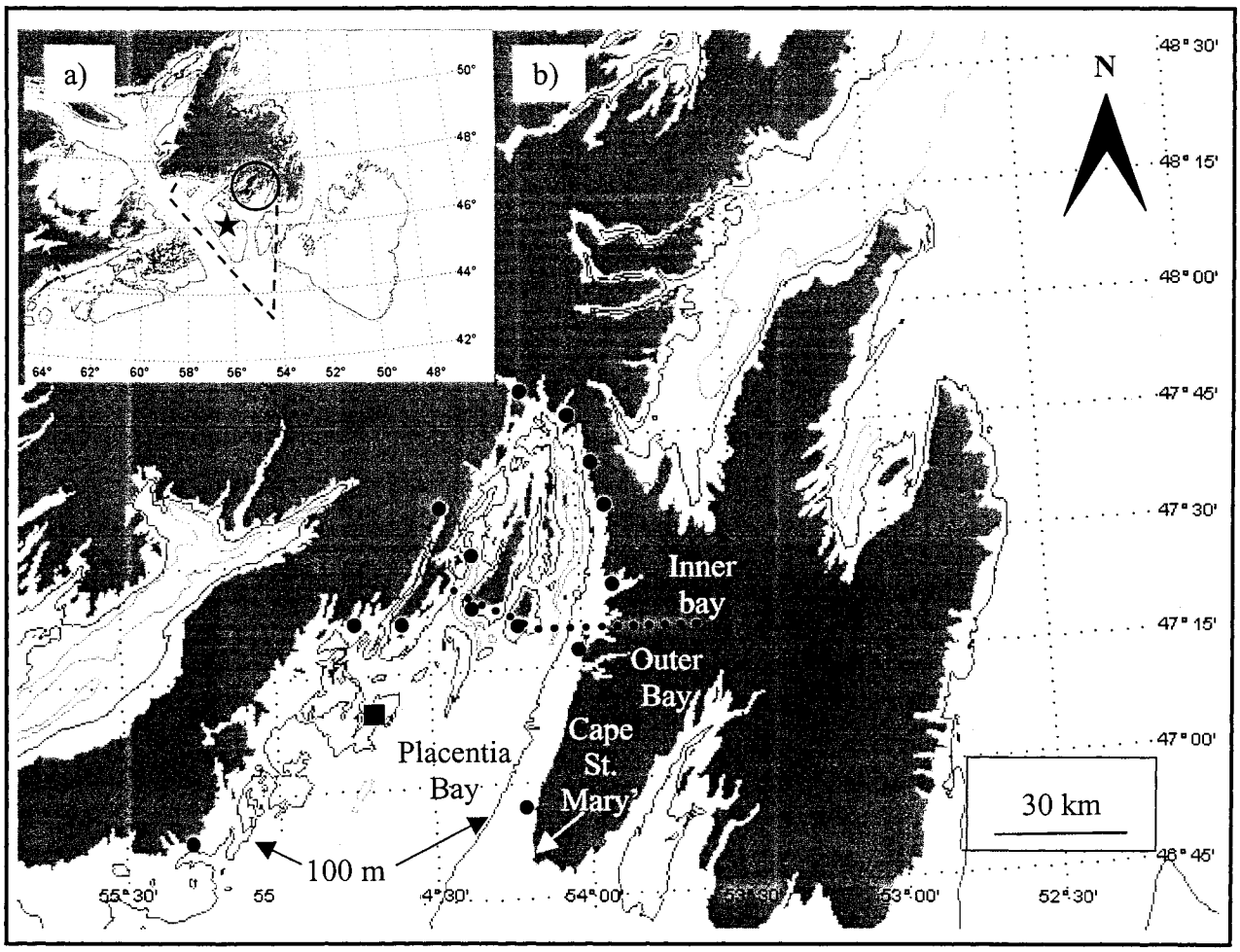

Figure 5.1 (a) East coast of North America showing the Northwest Atlantic Fisheries Organization (NAFO) subdivision 3Ps (dashed line) and Placentia Bay (inside circle) on the south coast of Newfoundland and (b) detailed view of the bay showing 100 m depth contour (indicated by black arrow) which represents the limit of acoustic sampling. Black dots represent the locations from where reported commercial fisheries operated. The dotted line across the bay indicates the division between the inner and outer bay. ■ = Oderin Bank and ★ = St. Pierre Bank.

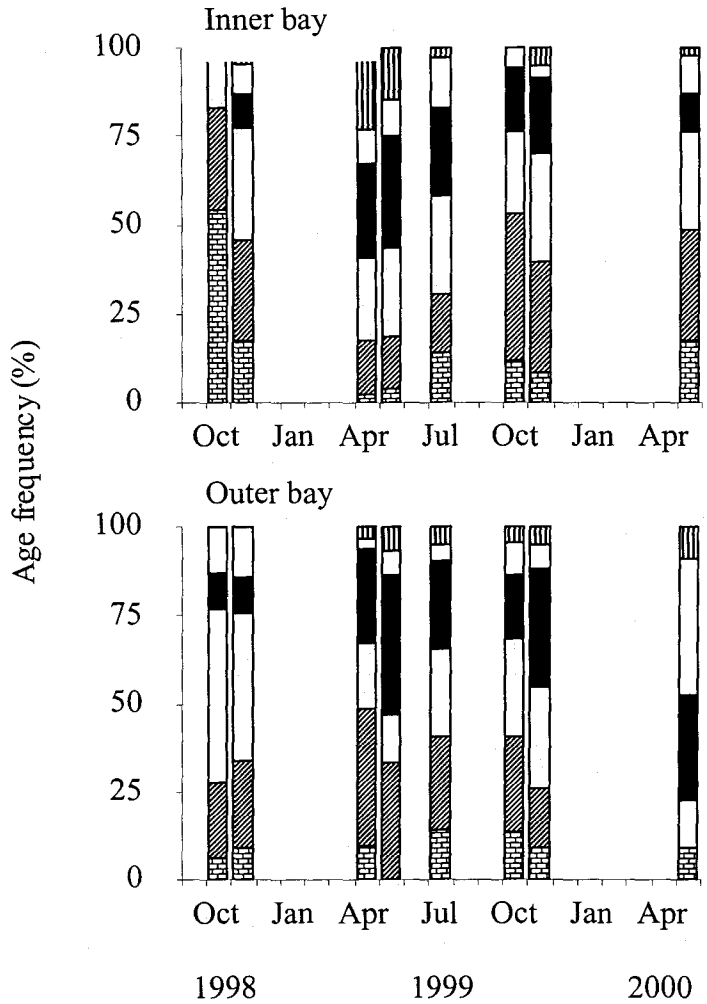

Figure 5.2 Age frequency distribution (%) of cod ages 4-9 sampled during acoustic surveys in Placentia Bay (n = 1716). = age 4, = age 5, = age 6, = age 7, = age 8, and = age 9.

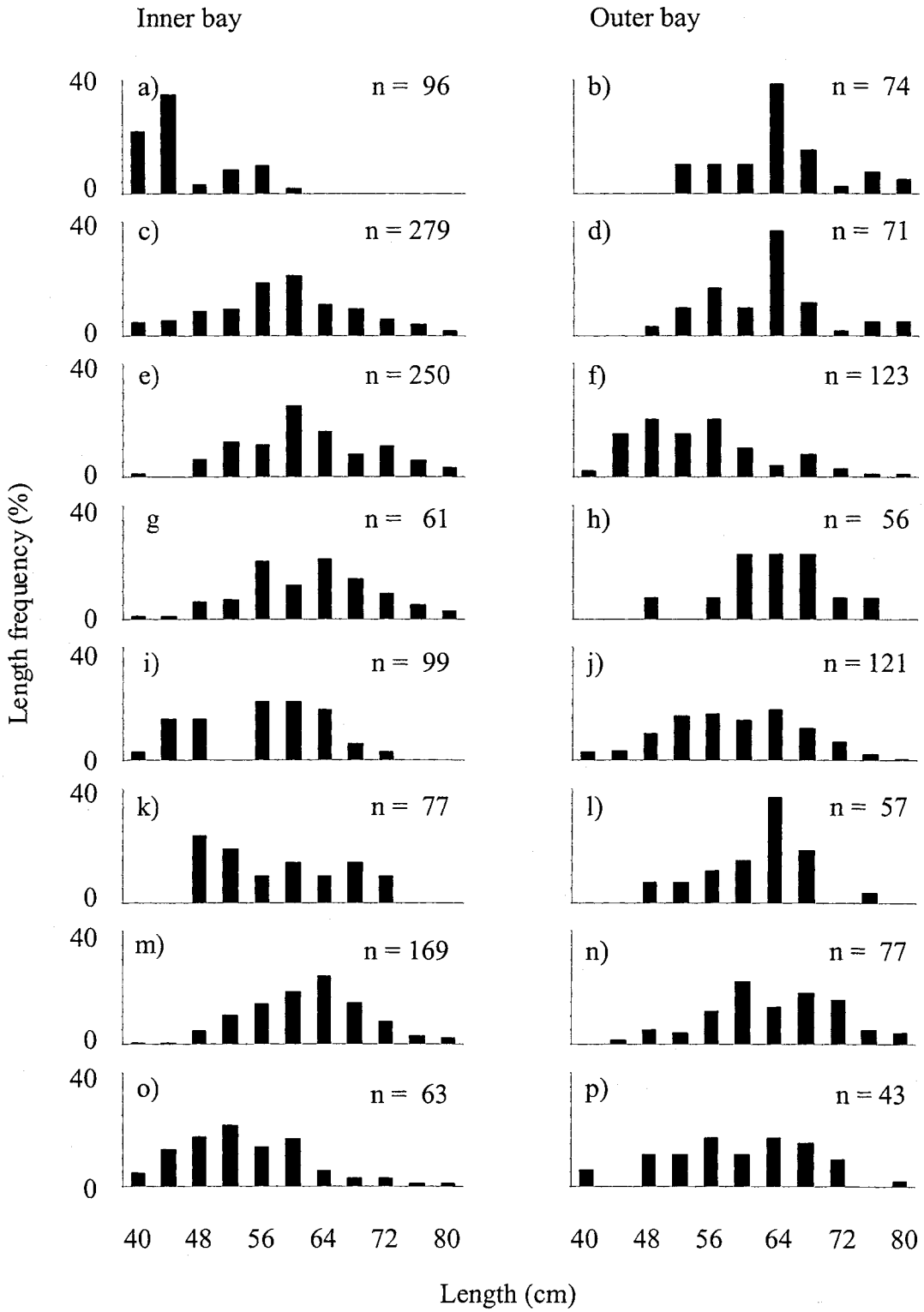

Figure 5.3 Length frequency distribution (%) of cod length classes 40-80 cm sampled during surveys in Placentia Bay. 1998: (a-b) October, (c-d) November; 1999: (e-f) April, (g-h) May, (i-j) July, (k-l) October, (m-n) November; 2000 (o-p) May.

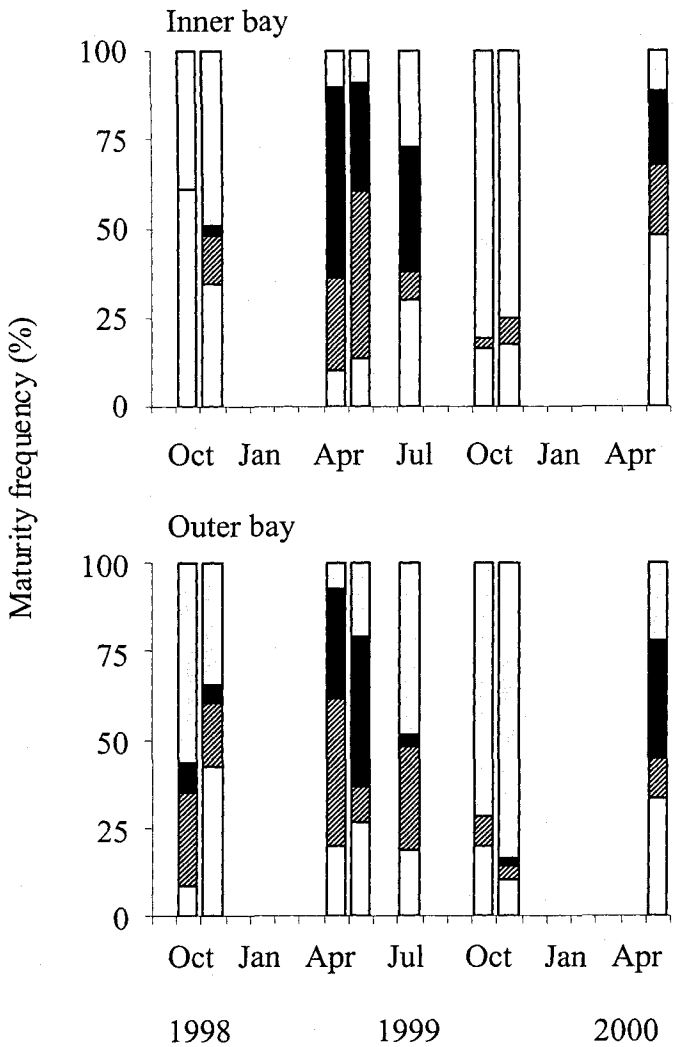

Figure 5.4 Maturity stage frequency distribution (%) of cod ages 4-9 (males and females combined) sampled during acoustic surveys in Placentia Bay (n =1716). Maturity stages defined in text. ☐ = immature, ▨ = pre-spawning, ■ = spawning and ☐ = spent.

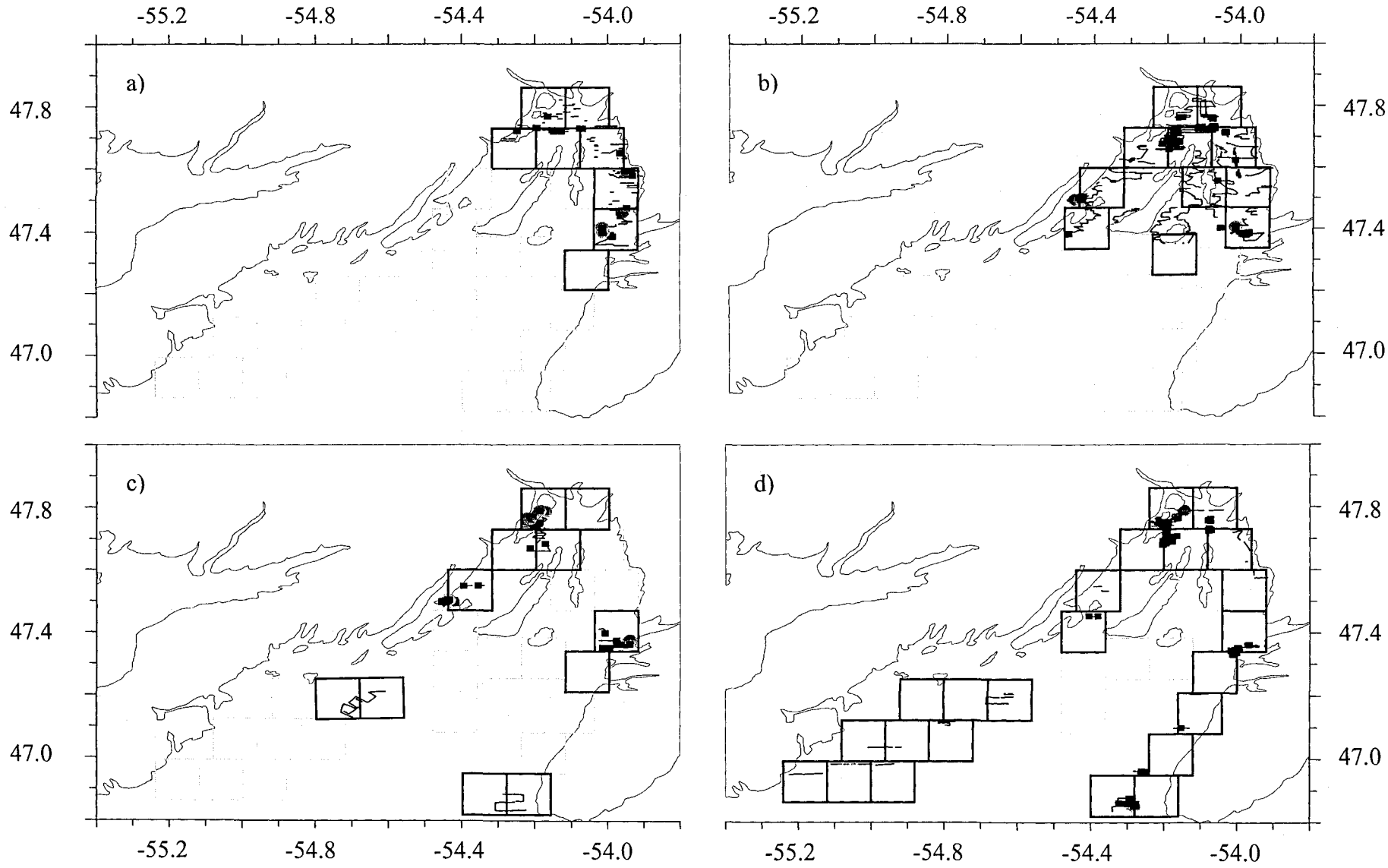

Figure 5.5 Transect track and cod density distribution estimated from acoustic surveys in Placentia Bay during 1998 (a = October, b = November), 1999 (c = April, d = May, e = July, f = October, g = November) and 2000 (h = May). Dotted line (< 0.01 fish.m^{-2}), square (≥0.01 and < 0.1 fish.m^{-2}) and red circle ≥0.1 fish.m^{-2}). Square grid = sampling blocks used to run acoustic transects (one block = 120 km^2) and black square = acoustically sampled block.

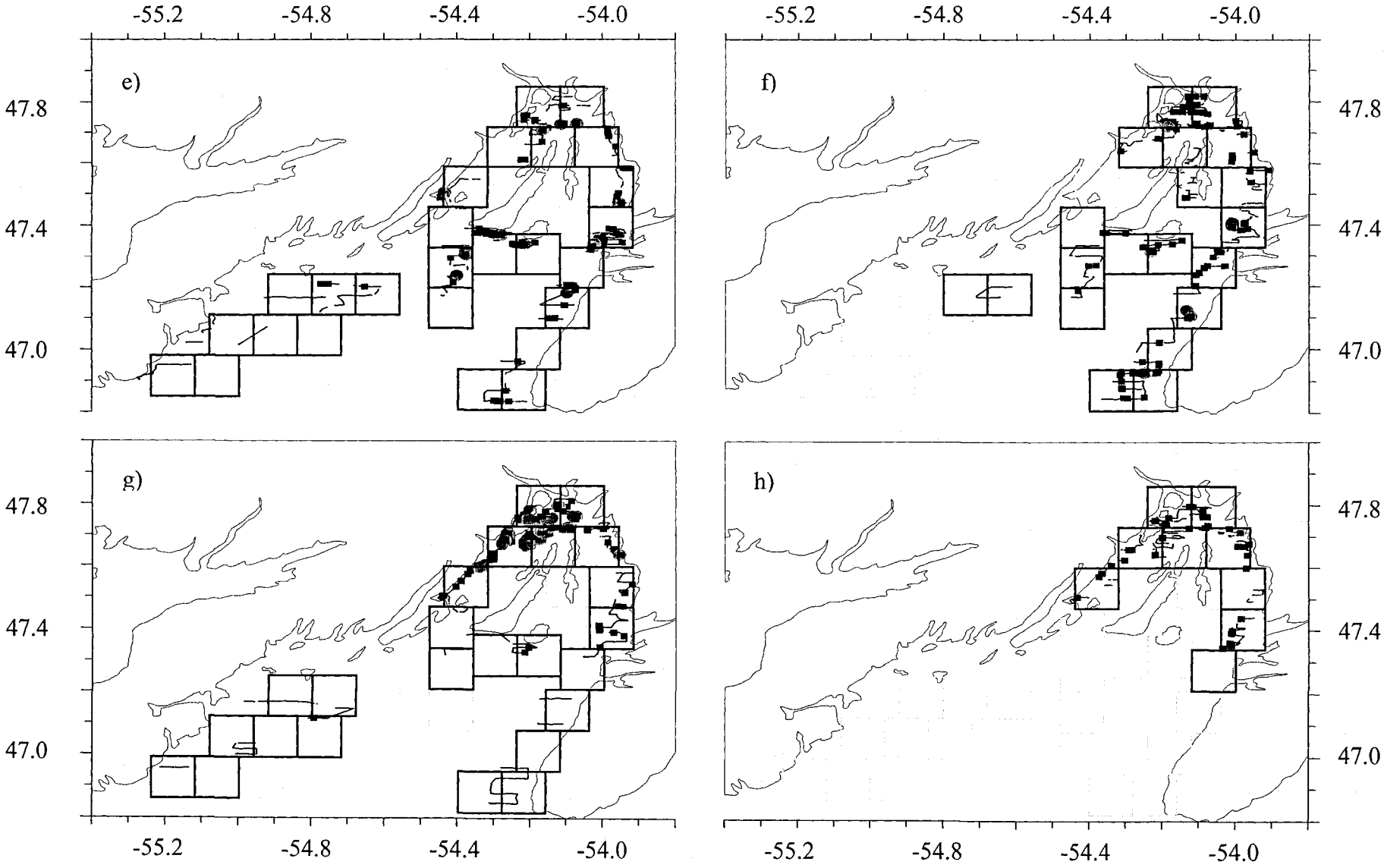

Figure 5.5 (cont.) Transect track and cod density distribution estimated from acoustic surveys in Placentia Bay during 1998 (a = October, b = November), 1999 (c = April, d = May, e = July, f = October, g = November) and 2000 (h = May). Dotted line (< 0.01 fish.m^{-2}), square (≥0.01 and < 0.1 fish.m^{-2}) and red circle ≥0.1 fish.m^{-2}). Square grid = sampling blocks used to run acoustic transects (one block = 120 km^2) and black square = acoustically sampled block.

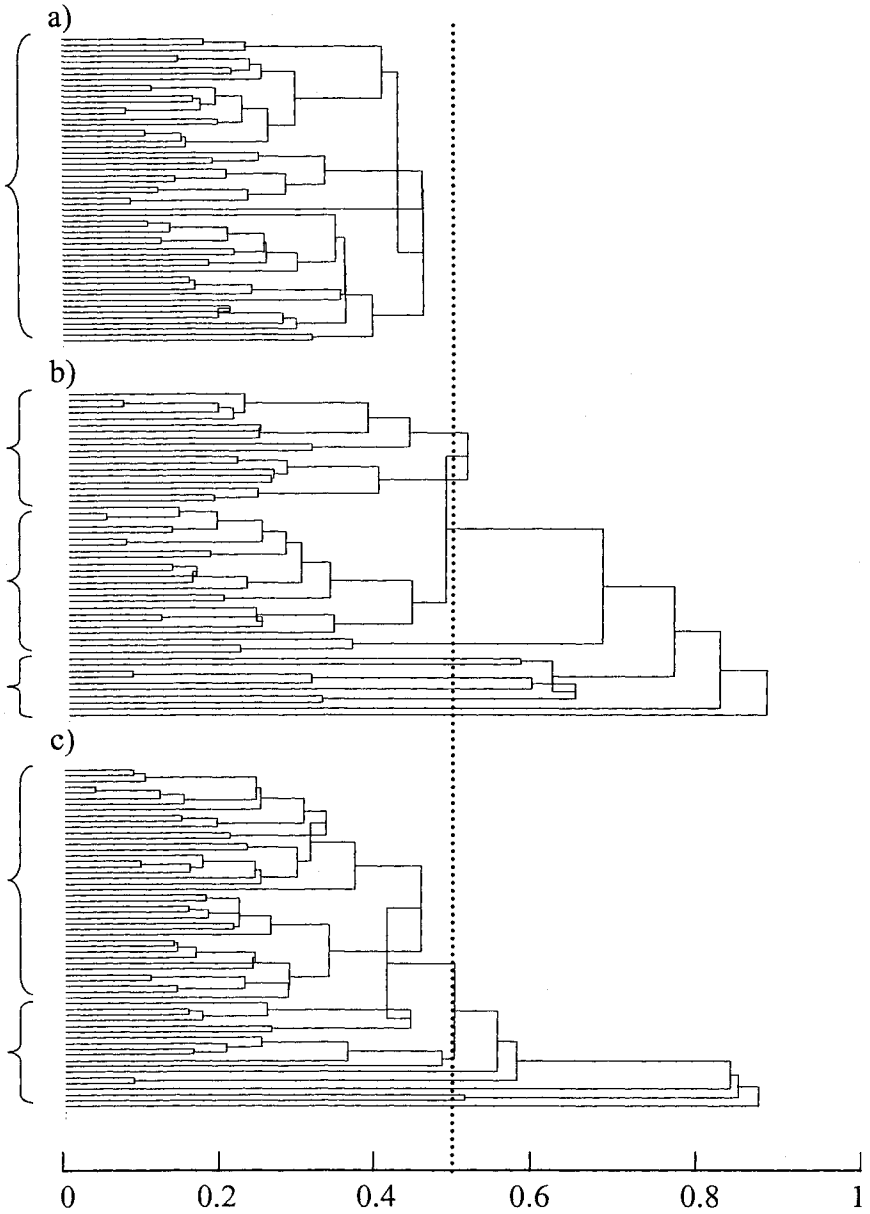

Fig. 5.6 Examples of dendrograms produced by cluster analysis of biological traits of Placentia Bay cod during 1999: (a) age 6 in April (inner bay), (b) age 7 in July (outer bay) and (c) age 6 in November (inner bay). Variables used in the analysis (defined in text) include somatic weight, gonado-somatic index, Fulton's K condition factor and hepato-somatic index of each fish sampled (represented by horizontal lines in dendrograms). Each bracket shows an identified cluster at distances > 0.5 between centroids (vertical dotted line).

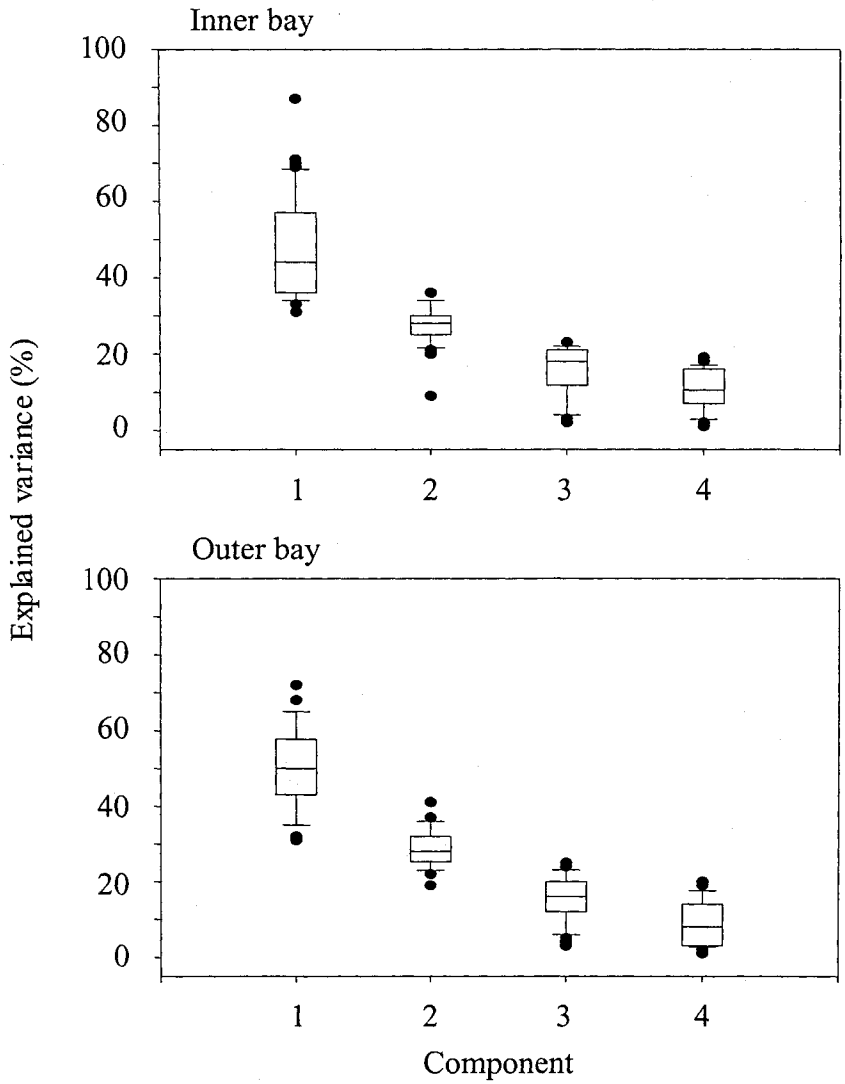

Figure 5.7 Box plot of the percentage of the explained variance by 1-4 components used in the cluster analysis (all combinations of ages and surveys). The grey box lower and upper limits represent the 25th and 75th percentiles, respectively, the line inside the box represents the median and the lower and upper limits of the T-bars the 10th and 90th percentiles, with values beyond this range represented by black dots.

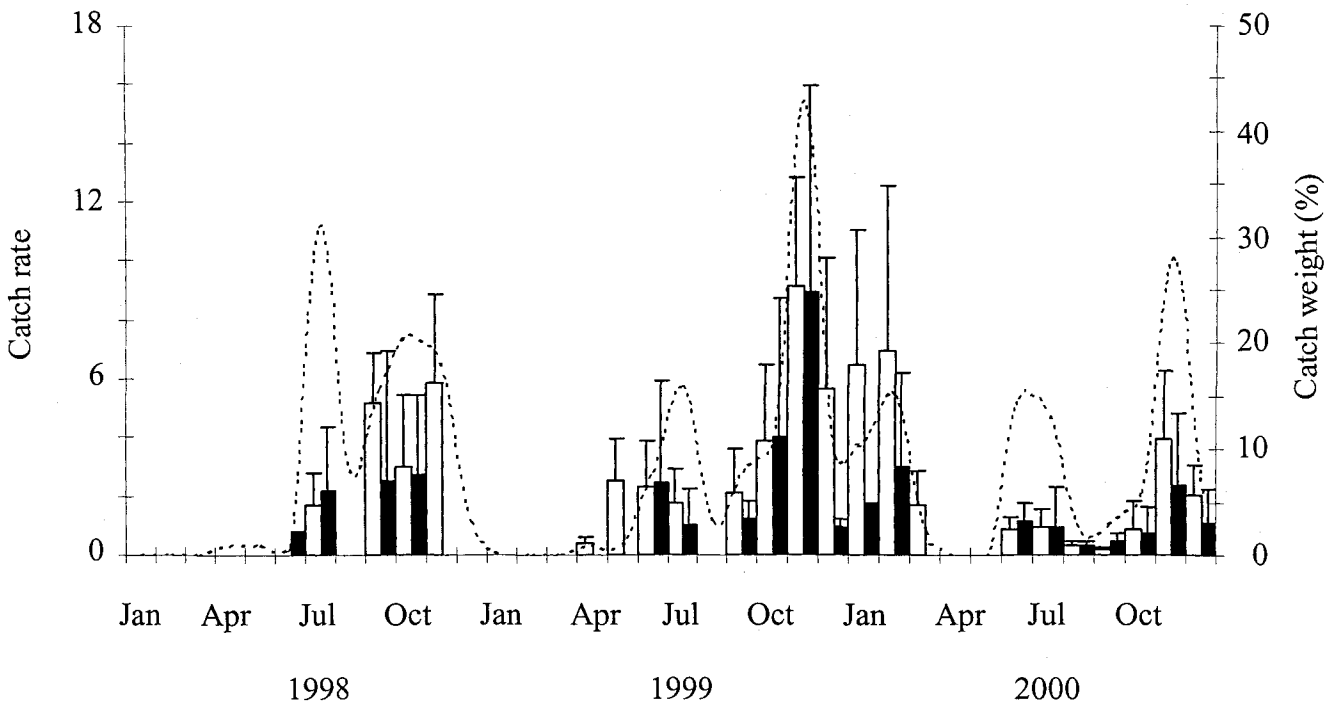

Figure 5.8 Catch rate (mean and SD) estimated as catch weight (t) landed monthly by one fisherman (bar) and proportion of catch weight landed monthly by the commercial cod fishery in Placentia Bay (dotted line) during 1998-2000. Catch rate data are from purchase slips (National Sea Products, Arnold's Cove, Placentia Bay). Catch weight data are from Brattey *et al.* (1999, 2000 and 2001). Open bar = inner bay, black bar = outer bay and T-bar = SD.

Chapter 6 Using simulations to develop sustainable harvest strategies for Placentia Bay cod (*Gadus morhua*)

6.1 Abstract

Atlantic cod (*Gadus morhua*) fished in Placentia Bay, Newfoundland, may include fish from a resident population and non-resident migratory fish that move into the bay during the post-spawning period. The migration and mixing of different groups of fish in the bay results in large within-year variations in abundance and age composition of the stock. In this study, I evaluated the effects of various harvest strategies on sustainability of cod in Placentia Bay. Five levels of fishing mortality (F) on stock biomass and catch trends over a 10-year period were simulated. Simulations were based on stock abundance and age composition data derived from seasonal acoustic surveys of Placentia Bay. Initial maximum catches were obtained by harvesting cod ages 4-6, but this resulted in stock decline or collapse. Using recent stock-recruitment data from Placentia Bay, stock growth and sustainability resulted from low-moderate harvest rates (20-30%) on all ages or on older fish (ages 6-9). Harvest rates above this threshold resulted in pronounced stock decline in most cases. The simulation results suggest that stock growth and catch yield of Placentia Bay cod is driven by the survival of younger fish and by allowing age diversity in the stock, which appears to facilitate good recruitment, particularly when abundance is high. The simulations showed that the smaller resident component of the stock as observed during the fall could sustain alone a fishery. In addition, a fall fishery would harvest fish in top physiological condition, which translates in maximum catch yield and profitability to the industry. However, the mixed stock scenarios (as observed in late spring and summer) were the most productive and resulted in the largest sustainable catches. Fisheries conducted on spawning aggregations and on younger fish are to be

avoided as they are least sustainable, have lower profitability and may disrupt spawning activities. The simulations showed that it is not only the level of F that will impact trends in abundance, but how F is distributed across age groups, which will impact stock performance.

6.2 Introduction

In recent decades, many cod stocks, including those in Atlantic Canada (FRCC, 2003a, 2003b, and 2003c), Greenland, Iceland, the Baltic and North Sea (Brander, 1994; Anon., 2000) have declined to low abundance levels and resulting in the collapse of some stocks and the announcement of fishing moratoria (Myers *et al.*, 1997a; Rätz, 1997; Fu *et al.*, 2001). In the northwest Atlantic, the factors believed to have contributed to the decline of the cod stocks include overfishing (Hutchings and Myers, 1994; Myers *et al.*, 1997b), or the combined effects of overfishing and environmental factors (Dutil *et al.*, 1999; Rose *et al.*, 2000). Notwithstanding the reasons, the present status of most of these stocks attests to the difficulties in assessing cod abundance and the impact of fisheries.

If relevant information on stock abundance, biology and fishery data are available, simulations become a useful tool for stock assessment and management (Fromentin and Fonteneau, 2001; Gerber *et al.*, 2002; Post *et al.*, 2003). Simulations provide a means by which the consequences of various alternative management strategies may be evaluated.

In this study, I use simulations to investigate stock abundance and catch trends of a cod fishery using stock scenarios (stock abundance and age composition) derived from seasonal acoustic surveys of Placentia Bay, Newfoundland. The cod stock fished in Placentia Bay may include both a resident population that spawns in the bay and non-resident migratory fish that spawn on St. Pierre Bank and in Fortune Bay (Templeman, 1979; Davis *et al.*, 1994; Lawson and Rose, 2000). The migrations and mixing of

different groups of fish in the bay results in large within-year variations in abundance indices and age composition of the stock (Mello and Rose, 2005a and 2005b). The objectives of this study are to examine through simulations (1) the effect of various harvest strategies, specifically age dependent fishing mortality and harvest levels on the sustainability of Placentia Bay cod and (2) examine how the outcome of such strategies are effected by variability in stock abundance and composition.

6.3 Material and Methods

6.3.1 Fishery

Placentia Bay is part of the NAFO subdivision 3Ps cod management area (Figure 6.1) that has been a centre for Atlantic cod fisheries since the early 16th century (Lear, 1998). Harvesting of cod in 3Ps has occurred during all seasons using gillnet (now the dominant gear), handline, baited longline, otter trawl and cod trap (Davis *et al.*, 1994). Total reported landings in 3Ps declined from 59,000 t in 1987 to 36,000 t in 1992 and a moratorium on cod fishing was imposed in 1993 after 15,000 t had been landed. The fishery reopened in 1997 and since then the total allowable catch (TAC) has ranged from 10,000-30,000 t and is currently 15,000 t (FRCC, 2003a). Historical catches in Placentia Bay are not known, but in the post-moratorium period reported landing in the bay ranged from 5,700 t (1998) to 11,600 t (1999) representing from 30% (2002) to 50% (1997) of the total reported catch in 3Ps (Brattey *et al.*, 2003).

6.3.2 Surveys

During 1999 five acoustic surveys were conducted in Placentia Bay in April, May, July, October and November. Surveys employed a Biosonics DT 4000 echosounder with a 120 kHz transducer mounted on a towed body. The system was calibrated with a tungsten-carbide sphere according to standard procedures (Foote *et al.*, 1987). Acoustic data (echograms) were edited manually and integrated using FASIT software (Lefeuvre *et al.*, 2000) to determine an area backscattering coefficient and from which a fish density estimate was obtained for each 100 m of transect track in areas < 120 m depth (see Figure 5.5).

Cod were caught by handline from acoustically identified aggregations during all surveys. Handlining was conducted for 30 minutes using four lines each having six equal sized unbaited hooks (10.2 cm long by 2.6 cm wide). The small number of samples of younger and older fish limited analyses to cod ages 4-9. For these age groups a total of 1090 fish were sampled for total length, total weight, somatic weight (total weight – organ weight), gonad weight, sex, maturity stage and otoliths for age determination. Cod length and weight were measured to the nearest cm and g, respectively. Age, length, weight, sex and maturity stage distribution were calculated using data from all fishing sets pooled by survey and stratum (see Mello and Rose, 2005a, 2005b and 2005c).

A fish density index (mean fish density) was obtained for each survey and stratum using geostatistics. Ordinary kriging was used to interpolate fish density. An estimation of

abundance in number was obtained by multiplying the density index (fish.m^{-2}) by the stratum area (1.2 x 10^9 m^2 and 2.4 x 10^9 m^2 for the inner and outer bay, respectively). Biomass estimate was obtained by scaling the abundance in number by the age frequency distribution and mean total weight at age of catches obtained during the surveys (Table 6.1). Details on survey design, acoustic and geostatistical analyses and abundance estimation can be found in Mello and Rose (2005d).

6.3.3 Simulations

Simulations were used to compare abundance and catch trajectories resulting from different allocations of fishing mortality (referred to herein as fishing strategy). Fishing strategies were chosen to mimic the effect of different gear and fishing regimes. Because of the large intra-annual variability in abundance indices and other biological traits resulting from seasonal mixing of various stock components (Chapter 5), five different stock abundance scenarios were considered (S_1-S_5). For each scenario the abundance in number ($\sum N_{a,0}$) and biological characteristics of the stock used to start the simulations were based on the seasonal surveys in spring (April-May), summer (July) and fall (October-November) of 1999. These were assumed to represent the range of stock biomass and age compositions of cod found in the bay during different seasons. Although the simulations consider biological traits and stock abundance as observed at different seasons in 1999, the simulations do not account directly for timing of harvesting on the stock.

Twenty iterations of each combination of fishing strategy and stock abundance and age composition (scenario) were run tracking stock abundance and catch over a 10-year period. The time-scale used was assumed to be equivalent to the passage of one 'cod generation' through the fishery with sufficient time to capture strong cohort effects and changes resulted from harvest strategies (Fromentin *et al.*, 2000; Hutchings and Ferguson, 2000). Larger scale projections were not considered useful as abundance on these scales may well be influenced by effects other than fisheries such as long-term variations in the environment (Klyashtorin, 1998; Godø, 2003).

Abundance estimates (ages 4-9) in April-May (scenarios S_1-S_2) ranged from 4.5-11.1 million fish (10,000-27,900 t) mostly pre-spawning and spawning older fish (ages 7-9), in July (S_3) 17.8 million fish (35,600 t), comprised mostly of younger (4-6) and spent fish and in October-November (S_4-S_5) 5.6-6.5 million fish (14,000-15,300 t) in which the proportion of younger fish reached 77% in October but then declined in November as the proportion of older cod increased up to 46% (see Figures 2 and 4 in Mello and Rose, 2005d).

Assumptions used in the simulations include an age-independent instantaneous rate of natural mortality (M) of 0.2 and recruitment (number of fish that recruit to the stock) based on a linear relationship between potential fecundity and recruitment at age 3. This formulation allowed the simulations to be put into matrices framework with constant coefficients. Hence stock abundance and catch trajectories correspond to equilibrium projections and they are used for diagnostic purposes and not as predictions.

Five different fishing strategies (F_1-F_5) were used in the simulations (Table 6.1). F_1 used estimates of mortality at age similar to those from the 3Ps cod fishery in 1999 (Brattey *et al.*, 2000). This fishery was comprised of low-moderate harvest levels of cod ages 6-9. F_2 is 2 x F_1 (moderate-high fishing mortality on the same age groups as observed in F_1). The third and fourth strategies explored, F_3 and F_4, consisted of low-moderate and moderate-high mortality across all ages, respectively. F_5 consisted of moderate-high mortality on ages 4-6.

The simulations also mimic the effect of random variation in water temperature as a proxy for the influence of environmental condition on egg survival and annual recruitment. Water temperature has been linked to recruitment in cod (de Young and Rose, 1993; Ottersen and Sundby, 1995) and in other fishes with pelagic early life stages (Fréon and Misund, 1999; Cubillos and Arcos, 2002). For each iteration the environmental index at time t (i_t) was estimated as:

$$i_t = 0.03 + \log(1.7\,y) \qquad (1)$$

where 0.03 is the value of the April average temperature anomaly (°C) near the surface across the St. Pierre Bank (Figure 6.1) for the period 1955-2000 (Colbourne, 2002), 1.7 is a constant and y is a randomly generated number between 0 and 1. Equation (1) generates values ranging mostly from -0.2°C to 0.2°C. Values below -0.2°C were considered to represent cold years and assumed to be linked with below average recruitment, values between –0.2 and 0.2°C were considered average and values above 0.2°C were

considered warm and assumed to be linked with above average recruitment. This was then incorporated into the simulation by multiplying the expected recruitment by 0.6, 1 and 1.3, depending on whether the randomly generated temperature anomaly (i_t) was cold, average or warm. The coefficients 0.6 and 1.3 represent the percentage difference between the 25 and 75th percentiles and the average recruitment of 3Ps cod at age 3, respectively, during the period 1974-1999 (Brattey *et al.*, 2002).

Annual abundance projections employed an exponential survival model (Ricker, 1975). The set-up was based on an age structured and discrete temporal (yearly) model where stock biomass and catch projections (t) were estimated for each of the 10-year period and 20 iteration following a Monte Carlo approach. Stock collapse was declared when the stock biomass at the end of the simulation was < 20 % initial stock biomass. The evolution of a cohort between time t and t+1 ($N_{a+1,t+1}$) was calculated as:

$$N_{a+1,t+1} = N_{a,t} \, x \, p_{a,t} \qquad (2)$$

and the survival rate of cod age a at time t ($p_{a,t}$) is:

$$p_{a,t} = e^{(-(M+F_{a,t}))} \qquad (3)$$

where e is the base of natural logarithm. Recruitment was parameterised as:

$$N_{3,t+3} = \sum_{a=4}^{9} N_{a,t} \, x \, p_{a,t} \, x \, q_{a,t} \, x \, f_{a,t} \, x \, 0.000009 \, g_{a,t} \qquad (4)$$

where $N_{3,t+3}$ represents the number of recruits to the stock estimated at time t+3, q_a is the ratio female/male, f_a is the proportion of mature female and g_a is the number of eggs produced by an age a female. The coefficient 0.000009 represents the egg survival rate and was estimated based on a linear relationship ($r^2 = 0.57$, $n = 4$, $P < 0.01$) between cod abundance at age 3 and the total egg potential estimated for the spawning stock in Placentia Bay between 1996 and 1999 (Rose, unpublished data). N_3 for years 1 and 2 were assumed to be the same as $N_{3,t+3}$. The model proposed by Pinhorn (1984) for Placentia Bay cod was used to estimate g_a:

$$\log g_a = 5.52 + (0.84 \, x \log a) \qquad (5)$$

The stock biomass at time t (B_t) is calculated as:

$$B_t = \sum_{a=4}^{9} w_{a,t} \, x \, N_{a,t} \qquad (6)$$

where w_a is the mean total weight (kg) of cod age a. The catch number ($n_{a,t}$) and the catch rate ($u_{a,t}$) at age a and time t are:

$$n_{a,t} = u_{a,t} \, x \, N_{a,t} \qquad (7)$$

and

$$u_{a,t} = \left[\frac{F_{a,t}}{F_{a,t} + M} x \left(1 - e^{(-F_{a,t}+M)}\right) \right] \tag{8}$$

The catch biomass (b_t) and the overall harvest rate (h_t) are calculated as:

$$b_t = \sum_{a=4}^{9} w_{a,t} \, x \, n_{a,t} \tag{9}$$

and

$$h_t = \frac{b_t}{B_t} \tag{10}$$

6.4 Results

Temporal trends in stock biomass and catch projections were mostly of three types (Figure 6.2): (1) an initial decline or increase in abundance and catch followed by a steady-state trajectory in both cases, (2) an increase in abundance throughout the 10-year projection horizon, with an initial increase in catch followed by a steady-state trajectory and (3) a continuous decline in abundance (some times to levels < 20% of the initial biomass) and catch towards the end of the simulation period.

Annual stock biomass from the 10-year projections ranged mostly from 7,000-15,000 t in scenarios S_1, S_4 and S_5 and from 15,000-45,000 t in scenarios S_2-S_3 (Figure 6.3). These biomass projections had a range similar to that estimated from acoustic surveys in 1999 (10,000-35,800 t). Catch projections ranged mostly from 3,000-5,000 t in scenarios S_1, S_4 and S_5 to 5,000-10,000 t in scenarios S_2-S_3. Catch projections are consistent with the reported landings in Placentia Bay (5,000-11,000 t) during the post-moratorium period (Brattey *et al.*, 2003).

For each scenario, stock biomass levels were higher when low-moderate fishing mortality was applied to cod ages 6-9 (F_1) or to all ages (F_3). When moderate-high fishing mortality levels were applied to cod ages 6-9 (F_2) or to all ages (F_4) lower stock biomass levels were observed in all scenarios. Minimum abundance levels were observed when the fishery targeted cod ages 4-6 (F_5). Catch levels (within scenarios) on the other hand were largely similar for all fishing strategies (except F_5), as indicated by the small difference of the median values for catch. Variability of catch projections increased considerably in all scenarios when moderate-high fishing mortality was applied to younger fish (F_5) although no similar effect in catches occurred when moderate-high fishing mortality was directed at older fish (F_2) or to all ages (F_4). Catch variability also increased with increasing abundance levels.

On average, stock biomass stabilized or increased (up to 90%) over the projection horizon when the fishery harvested cod ages 6-9 (F_1-F_2) or was low to moderate for all ages (F_3) (Figure 6.4a). In such cases average harvest rates (i.e. percentage of the stock

removed annually by the fishery) were in the range of 20-30% (Figure 6.4b). Low to moderate declines in abundance (10-40%) were observed when the fishery targeted all age groups more intensively (F_4) with harvest rates mostly from 35-50%. A pronounced decline (60-80%) in stock biomass and in some occasions stock collapse resulted when the fishery targeted cod ages 4-6 (F_5). The average harvest rates in these cases were in excess of 50%.

6.5 Discussion

Despite differences in overall abundance and age composition among scenarios, the effect of various fishing strategies were similar, with low-moderate fishing mortality resulting in stock growth or sustainability (i.e., stock conservation and stable catches) over a 10-year period (one generation), but moderate-high mortality resulting in abundance decline, particularly when targeting younger fish.

Although the simulations take into account a wide range of abundance levels and differences in biological traits, which correspond to the stock mix present in the bay during spring, summer and fall, the scenarios assumed there to be only one stock component. However, tagging and other studies (Templeman, 1979; Davis *et al.*, 1994; Lawson and Rose, 2000) have shown that Placentia Bay contains a mix of stock components that vary seasonally. These components include a local population that spawns mainly in the inner parts of the bay in spring and non-resident fish, mostly from adjacent bays and offshore banks within 3Ps, that move into the bay during late spring

and summer and moving out again toward the end of the summer or later (Chapter 5). Unfortunately the relative abundance and catch rates of the various stock components at different periods of the year cannot be specified with any precision. This is due in part to the complexity of seasonal migration patterns as described above, but also due to the fact that at present there is no easily applied method for determining stock component affiliation of catches. Ideally, differential exploitation of stock components would be examined in the present simulations, but this was not feasible.

Despite the above cautions, some speculations as to the potential for differential exploitation maybe warranted. The 1999 estimates of abundance increased 2-4 fold from April through May-July, followed by an equivalent decrease during October-November (Mello and Rose, 2005d). These changes were followed by changes in size (age) composition, fish condition including reproductive condition (Mello and Rose 2005b and 2005c). Cod caught in July and November were comprised of a larger proportion of smaller (poor condition) and larger (top condition) fish, respectively. As a result, the fish present in the bay during April, October and November (S_1, S_4 and S_5) are most likely dominated by fish of the residential stock component, whereas those in May and July (S_2-S_3) are thought to represent a mixed stock comprised of resident and non-resident fish.

The simulations show that at 1999 abundance levels the residential stock should be able to sustain the actual fishing mortalities (F_1) as well as those presented in F_2 (targeting older fish) and F_3 (low-moderate for all ages). However, the resident stock could not withstand most moderate-high fishing mortality strategies (F_4-F_5). As expected high

abundance scenarios produced the highest catch levels. However, even with the highest initial abundances, moderate-high mortality strategies resulted in considerable stock decline. An increased risk of collapse occurred when younger fish were targeted. This outcome was consistent among all abundance scenarios (resident and mixed).

Targeting younger fish produced short term high (> 10,000 t) but overall variable catches (i.e., large range of values) through the simulation period. The simulation results suggest that stock biomass and catch yield of Placentia Bay cod is driven by the survival of younger fish and by a wide age diversity of fish which appears to facilitate good recruitment in cod stocks (Marteinsdottir and Thorarinsson, 1998; Chen and Mello, 1999). These effects are likely underestimated as cod normally get older than age 9 (oldest age in this study) and because a higher frequency of older spawners may also lead to higher recruitment (Marteinsdottir and Thorarinsson, 1998; Scott *et al.*, 1999). In a related study Pope (2004) used length-based delay-difference models to simulate long-term steady states of the yield of the 3Ps cod stock (which include Placentia Bay cod). He found that the main effect on yield was through recruitment of small fish to the fishery.

The results of this study also emphasise the importance of age structure in catches. For instance, targeting older fish (F_1-F_2) in scenario S_4 resulted in average harvest rates of 29-35% during a 10-year period. Such rates of removal were associated with an average 60% increase in biomass over the same period, whereas a similar harvest rate resulted in an 80% increase in biomass when low-moderate fishing mortality was applied to all ages (F_3). Likewise, in scenario S_2 harvest rates of 26-28% resulted in 10% decrease in

biomass when high fishing mortality was applied to older fish (F_2), but similar harvest rates resulted in 80% increase in biomass when fishing mortality was spread among ages (F_3).

The effect of stochastic variation (water temperature in this study) on recruitment was most evident for high stock abundance scenarios (S_2-S_3) as indicated by the wider range of values in biomass projections (i.e., good and bad recruitment years), particularly when the stock was subjected to low-moderate fishing mortality or high mortality of younger fish. The considerable differences in biomass levels and similarity of catches across most fishing strategies suggest that the interactions of stock specific attributes with fishing strategies had strong effect on recruitment. High fishing mortality resulted in similar or less variable recruitment (i.e., smaller range of values) in lower abundance scenarios (S_1, S_4 and S_5). Catches over a 10-year period were most variable when fishing heavily targeted younger fish. This was due to initially high catches followed by low ones, which appeared as recruitment started to fail.

Increased viability of cod stocks containing broader age structures is not unexpected. Spawning stocks with a more diverse age composition may result in protracted spawning (spatially and temporally) so that some early life stages may encounter more favourable environmental conditions for survival (Marteinsdottir and Petursdottir, 1995; Chen and Mello, 1999). In addition, traits such as fecundity, size of egg and larvae tend to be positively related to spawner size (Chambers and Waiwood, 1996; Kjesbu *et al.*, 1996; Trippel, 1998). As a result, the strength of a year-class may dependent to a large extent

upon favourable environmental conditions in cases where the size (age) composition of the spawning stock is reduced to a few classes of small (younger) fish, hence increasing temporal variation in recruitment (Chen and Mello, 1999), or when the stock abundance is high and comprised of many age groups (Marteinsdottir and Thorarinsson, 1998).

In most cases sustainable fishery scenarios were observed when harvest rates < 30% were applied. This is consistent with historical data for 3Ps cod (DFO, 2000) as when harvest rates rose above this threshold during the early 1960s, mid 1970s, late 1980s and early 1990s stock abundance declined eventually leading to the imposition of a fishing moratorium in 1993. However, it should be noted that the harvest rates that are sustainable in the simulations depend on the recruitment, which is based on a model from Placentia Bay between 1996-1999 that may or may not hold up over time.

In 1999 the reported catch in Placentia Bay was approximately 11000 t (mostly ages 6-9), which corresponded to seasonal harvest rates between 5 and 33% (Mello and Rose, 2005d). In the simulations similar levels of exploitation resulted in a sustainable fishery only in scenario S_3 (highest stock biomass estimates). Notwithstanding, removal levels from more recent years (4000-9000 t, Brattey *et al.*, 2003) were sustainable in scenarios S_2, S_3 and S_5 (low-moderate fishing mortality).

In Placentia Bay the implementation of the various fishing strategies explored in these simulations might be realized through allocation of quota to certain gear sectors. For instance the gear most commonly used (gillnet) preferentially harvest fish 60-90 cm in

length (Cadigan and Brattey, 2000). Other gears used in the fishery include the handline, which selects for fish > 60 cm, line trawl (> 80 cm) and trap (40-80 cm). Of all gears, the trap is likely to result in the largest diversity of sizes (ages) in catches and reduced mortality of older fish. These characteristics would be desirable for a fishery such as the one observed in 3Ps, as most of fish caught in the fishery have been 4-8 years old (40-70 cm) in recent years (DFO, 2003 and 2004). Historically, the trap fishery represented an important component of the inshore cod fishery in Newfoundland (Rose, 1992). From 1975-1993 traps accounted for an average of 18% of total landings in 3Ps, but after 1997 trap catches have been practically nil (Brattey *et al.*, 2002). Although trap fisheries are only practical during spring-summer (the capelin season), new types of gear with trap-like selectivity (e.g., cod pots) may prove useful.

According to the findings of this study, management recommendations for a sustainable cod fishery in Placentia Bay should include applying low-moderate harvest rates (20-30%) and fishing mortality targeted across ages or at older fish. Mixed stock scenarios were the most productive and resulted in the largest catches. Results from scenarios in which it may be inferred that the residential stock component dominates suggest that this component alone could sustain a small fishery, particularly if conducted in the fall. A fall fishery may also be desirable because cod body condition is highest, then leading to better yields and increased profitability to industry (Mello and Rose, 2005b). A fall fishery also avoids disrupting springtime spawning activities. These results require a few caveats. It should be noted that the simulations are solely based on biological considerations and do not include social and economic aspects of the fishery. In addition,

there is no doubt that some assumptions used were arbitrary and oversimplifications were needed (e.g., age-independent natural mortality, stock-recruitment). Nevertheless, simulations are thought to provide a useful tool to assist in the development of sustainable harvest strategies, such as identifying sustainable harvest rate thresholds and quantifying stock performance in relation to age dependent fishing mortality.

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6.7 References

Anon., 2000. Review of the stocks. ICES Advisory Committee on Fishery Management (ACFM). Fish Stock Assessment Working and Study Group Report (2000).

Brander, K.M. 1994. Spawning and life history information for North Atlantic cod stocks. ICES Cooperative Research Report No. 205.

Brattey, J., Cadigan, N.G., Healey, B.P., Lilly, G.R., Murphy, E.F., Stansbury, D.E., and Mahé, J.-C. 2003. An assessment of the cod (*Gadus morhua*) stock in NAFO Subdivision 3Ps in October 2003. DFO Canadian Science Advisory Secretariat Research Document 2003/092.

Brattey, J., Cadigan, N.G., Healey, B.P., Lilly, G.R., Murphy, E.F., Shelton, P.A., Stansbury, D.E., and Mahé, J.-C. 2002. An assessment of the cod (*Gadus morhua*) stock in NAFO Subdivision 3Ps in October 2002. DFO Canadian Science Advisory Secretariat Research Document 2002/96.

Brattey, J., Cadigan, N.G., Lilly, G.R., Murphy, E.F., Shelton, P.A., and Stansbury, D.E. 2000. An assessment of the cod stock in NAFO Subdivision 3Ps in October 2000. DFO Canadian Science Advisory Secretariat Research Document 2000/134.

Cadigan, N., and Brattey, J. 2000. Lower bounds on the exploitation of cod (*Gadus morhua*) in NAFO Divisions 3KL and Subdivision 3Ps during 1997-1999 from tagging experiments. DFO Canadian Science Advisory Secretariat Research Document 2000/73.

Chambers, R.C., and Waiwood, K.G. 1996. Maternal and seasonal differences in egg size and spawning characteristics of captive Atlantic cod, *Gadus morhua*. Canadian Journal of Fisheries and Aquatic Sciences, 53: 1986-2003.

Chen, Y., and Mello, L.G.S. 1999. Growth and maturation of cod (*Gadus morhua*) of different year classes in the Northwest Atlantic, NAFO subdivision 3Ps. Fisheries Research, 42: 87-101.

Colbourne, E. 2002. Oceanographic conditions in NAFO Subdivisions 3Pn and 3Ps during 2001 with comparisons to the previous year and the long-term (1971-2000) average. DFO Canadian Science Advisory Secretariat Research Document 2002/24.

Cubillos, L.A., and Arcos, D.F. 2002. Recruitment of common sardine (*Strangomera bentincki*) and anchovy (*Engraulis ringens*) off central-south Chile in the 1990's and the impact of the 1997-1998 El Nino. Aquatic Living Resources, 15: 87-94.

Davis, M.B., Lundrigan P., and Ripley, R. 1994. A description of cod stock structure in Placentia Bay, NAFO Subdivision 3Ps. DFO Atlantic Fisheries Research Document 94/32.

DFO, 2000. Subdivision 3Ps cod. DFO Stock Status Report A2-02 (2000).

de Young, B., and Rose, G.A. 1993. On recruitment and distribution of Atlantic cod (*Gadus morhua*) off Newfoundland. Canadian Journal of Fisheries and Aquatic Sciences, 50: 2729-2741.

Dutil, J.-D., Castonguay, M., Gilbert, D., and Gascon, D. 1999. Growth, condition, and environmental relationships in Atlantic cod (*Gadus morhua*) in the northern Gulf of St. Lawrence and implications for management strategies in the Northwest Atlantic. Canadian Journal of Fisheries and Aquatic Sciences, 10: 1818-1831.

Foote, K.G., Knudsen, H.P., and Vestnes, G. 1987. Calibration of acoustic instruments for fish density estimation: a practical guide. ICES Cooperative Research Report 144.

FRCC (Fisheries Resource Conservation Council), 2003a. 2003/2004 conservation requirements for groundfish stocks on the Scotian Shelf and in the Bay of Fundy (4VWX5Z), in Sub-areas 0, 2+3 and redfish stocks. Report to the Minister, FRCC. 2003, R.1, January 2003, 120pp.

FRCC (Fisheries Resource Conservation Council), 2003b. 2003/2004 conservation requirements for 2J3KL cod stocks. Report to the Minister, FRCC. 2003, R.2, March 2003, 20pp.

FRCC (Fisheries Resource Conservation Council), 2003c. 2003/2004 conservation requirements for groundfish stocks in the Gulf of St. Lawrence. Report to the Minister, FRCC. 2003, R.3, April 2003, 50pp.

Fréon, P., and Misund O.A. 1999. Dynamics of pelagic fish distribution and behaviour: effects on fisheries and stock assessment. Blackwell Science Ltd., Cambridge.

Fromentin, J.-M., and Fonteneau, A. 2001. Fishing effects and life history traits: a case study comparing tropical versus temperate tunas. Fisheries Research, 53: 133-150.

Fromentin, J.-M., Gjøsæter, J., Bjørnstad, O.N., and Stenseth, N.C. 2000. Biological processes and environmental factors regulating the dynamics of the Norwegian Skagerrak cod populations since 1919. ICES Journal of Marine Science, 57: 330-338.

Fu, C., Mohn, R., and Fanning, L.P. 2001. Why the Atlantic cod (*Gadus morhua*) stock off eastern Nova Scotia has not recovered. Canadian Journal of Fisheries and Aquatic Sciences, 58: 1613-1623.

Gerber, L.R., Kareiva, P.M., and Bascompte, J. 2002. The influence of life history attributes and fishing pressure on the efficacy of marine reserves. Biological Conservation, 106: 11-18.

Godø, O.R., 2003. Fluctuation in stock properties of north-east Arctic cod related to long-term environmental changes. Fish and Fisheries, 4: 121-137.

Hutchings, J.A., and Ferguson, M. 2000. Temporal changes in harvesting dynamics of Canadian inshore fisheries for northern Atlantic cod, *Gadus morhua*. Canadian Journal of Fisheries and Aquatic Sciences, 57: 805-814.

Hutchings , J.A., and Myers, R.A. 1994. What can be learned from the collapse of a renewable resource? Atlantic cod, *Gadus morhua*, of Newfoundland and Labrador. Canadian Journal of Fisheries and Aquatic Sciences. 51: 2126-2146.

Klyashtorin, L.B. 1998. Long-term climate change and main fish production in the Atlantic and Pacific. Fisheries Research, 37: 115-125.

Kjesbu, O.S., Kryvi, H., and Norberg, B. 1996. Oocyte size and structure in relation to blood plasma steroid hormones in individually monitored, spawning Atlantic cod. Journal of Fish Biology, 49: 1197-1215.

Lawson, G.L., and Rose, G.A. 2000. Seasonal distribution and movements of coastal cod (*Gadus morhua*) in Placentia Bay, Newfoundland. Fisheries Research, 49: 61-75.

Lear, W.H. 1998. History of fisheries in the Northwest Atlantic: The 500-year perspective. Journal of Northwest Atlantic Fisheries Organization, 23: 41-73.

Lefeuvre, P., Rose, G.A., Gosine, R., Hale, R., Pearson, W., and Khan, R. 2000. Acoustic species identification in the Northwest Atlantic using digital image processing. Fisheries Research, 47: 137-147.

Marteinsdottir, G., and Thorarinsson, K. 1998. Improving the stock-recruitment relationship in Icelandic cod (*Gadus morhua*) by including age diversity of spawners. Canadian Journal of Fisheries and Aquatic Sciences, 55: 1372-1377.

Marteinsdottir, G. and Petursdottir, G. 1995. Spatial and temporal variation in reproduction of Icelandic cod at Selvogsbanki and nearby coastal areas. ICES CM 1995/G:15.

Mello, L.G.S., and Rose, G.A. 2005a. Using geostatistics to quantify seasonal distribution and aggregation patterns of fishes: an example of Atlantic cod (*Gadus morhua*). Canadian Journal of Fisheries and Aquatic Sciences, 62: 659-670.

Mello, L.G.S, and Rose, G.A. 2005b. Seasonal cycle in weight and condition in Atlantic cod (*Gadus morhua* L) in relation to fisheries. ICES Journal of Marine Science, 62: 1006-1015.

Mello, L.G.S., and Rose, G.A. 2005c. Seasonal growth of Atlantic cod (*Gadus morhua* L.): effects of temperature, feeding and reproduction. Journal of Fish Biology, 67: 149-170.

Mello, L.G.S., and Rose, G.A. 2005d. Seasonal variation in abundance and stock composition of Atlantic cod (*Gadus morhua* L.) in Placentia Bay, Newfoundland, in relation to fisheries. Fisheries Research, 74: 142-156.

Myers, R.A., Hutchings, J.A., and Barrowman, N.J. 1997a. Why do fish stocks collapse? The example of cod in Atlantic Canada. Ecological Applications, 7: 91-106.

Myers, R.A., Mertz, G., and Fowlow, P.S. 1997b. Maximum population growth rates and recovery for Atlantic cod, *Gadus morhua*. Fishery Bulletin, 95: 762-772.

Ottersen, G. and Sundby, S. 1995. Effects of temperature, wind and spawning stock biomass on recruitment of Arcto-Norwegian cod. Fisheries Oceanography, 4: 278-292.

Pinhorn, A.T. 1984. Temporal and spatial variation in fecundity of Atlantic cod (*Gadus morhua*) in Newfoundland waters. Journal of the Northwest Atlantic Fisheries Science, 5: 161-170.

Pope, J.G. 2004. Integrating climate variation and change into models of fisheries yield, with an example based upon the southern Newfoundland (NAFO Subdivision 3Ps) cod. *In* A. Payne, C. O'Brian, and S. Rogers (Ed.) Management of shared fish stocks pp. 279-302.

Post, J.R., Mushens, C., Paul, A., and Sullivan, M. 2003. Assessment of alternative harvest regulations for sustaining recreational fisheries: Model development and application to bull trout. North American Journal of Fisheries Management, 23: 22-34.

Rätz, H.-J. 1997. The development of the Atlantic cod off Greenland during the second half of the 20th century. Informationen fur die Fischwirtschaft, 44: 3-9.

Ricker, W.E. 1975. Computation and interpretation of biological statistics of fish populations. Fisheries Research Board of Canada 191.

Rose, G.A., de Young, B., Kulka, D.W., Goddard, S.V., and Fletcher, G.L. 2000. Distribution shifts and overfishing the northern cod (*Gadus morhua*): a view from the ocean. Canadian Journal of Fisheries and Aquatic Sciences, 57: 644-663.

Rose, G.A, 1992. Indices of total stock biomass in the "Northern" and Gulf of St. Lawrence Atlantic cod (*Gadus morhua*) stocks derived from time series analysis of fixed gear (trap) catches. Canadian Journal of Fisheries and Aquatic Sciences, 49: 202-209.

Scott, B., Marteinsdottir, G., and Wright, P. 1999. Potential effects of maternal factors on spawning stock-recruitment relationships under varying fishing pressure. Canadian Journal of Fisheries and Aquatic Sciences, 56: 1882-1890.

Templeman, W. 1979. Migration and intermingling of stocks of Atlantic cod, *Gadus morhua*, of the Newfoundland and adjacent areas from tagging in 1962-66. ICNAF Research Bulletin, 14: 5-50.

Trippel, E.A. 1998. Egg size and viability and seasonal offspring production of young Atlantic cod. Transactions of the American Fisheries Society, 127: 339-359.

6.8 Tables

Table 6.1 Input parameters used in simulations of the Placentia Bay cod fishery. F_1-F_5 are different rates of instantaneous fishing mortality. S_1-S_5 are abundance estimates in number from acoustic surveys conducted in Placentia Bay during April, May, July, October and November (1999) which are used to start the simulations. Weight at age refers to the mean total weight of cod sampled during surveys (inner and outer bay).

	Age					
	4	5	6	7	8	9
Fishing mortality						
F_1	0.05	0.14	0.43	0.55	0.51	0.25
F_2	0.10	0.28	0.86	1.10	1.02	0.50
F_3	0.12	0.21	0.30	0.44	0.32	0.23
F_4	0.21	0.50	0.58	0.68	0.33	0.21
F_5	0.64	0.55	0.48	0.17	0.05	0.05
Abundance ($\times 10^6$)						
S_1	0.37	0.90	0.91	1.04	0.48	0.79
S_2	0.76	2.04	2.63	3.60	1.34	1.74
S_3	2.30	4.53	4.72	4.00	1.27	1.08
S_4	0.59	1.16	1.56	1.66	0.36	0.31
S_5	0.55	2.16	1.87	1.43	0.21	0.28
Weight at age (kg)						
S_1	0.79-0.82	1.06-1.22	1.70-1.85	1.87-1.75	2.37-2.89	3.50-2.98
S_2	0.78-0.85	1.37-1.64	1.79-2.17	2.21-2.26	2.92-3.20	3.64-3.66
S_3	1.03-1.33	1.13-1.68	1.92-2.13	2.17-2.51	2.53-3.10	2.40-2.62
S_4	1.31-1.29	1.87-1.77	2.26-1.90	2.66-2.97	3.20-2.72	4.22-4.70
S_5	1.32-1.55	2.02-1.93	2.53-2.51	2.74-2.97	3.44-3.35	3.15-4.57

6.9 Figures

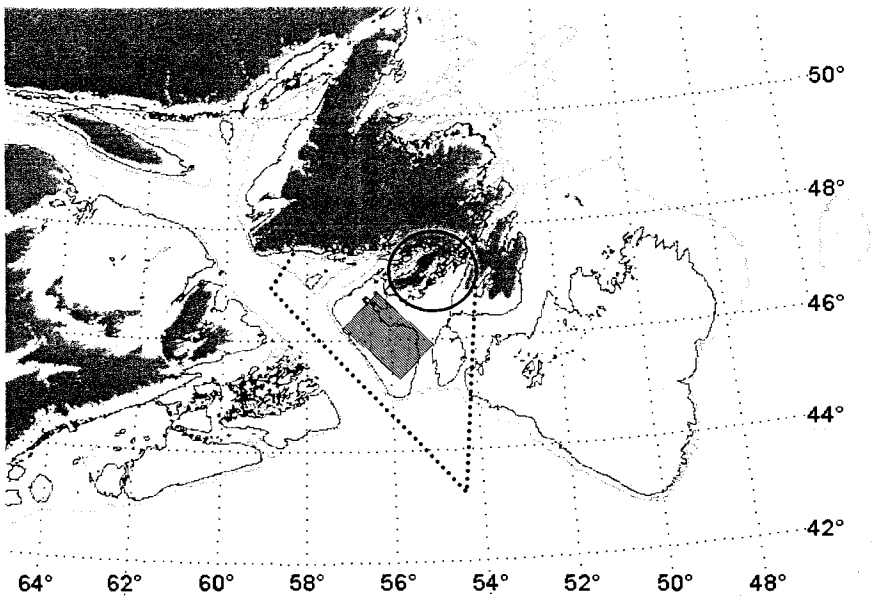

Figure 6.1 East coast of North America showing the Northwest Atlantic Fisheries Organization (NAFO) subdivision 3Ps (black dotted line) and Placentia Bay (inside circle) on the south coast of Newfoundland. The grey box represents the area where water temperature measurements were taken on the St. Pierre Bank and used to estimate the near surface temperature anomaly time series which were used in the simulations.

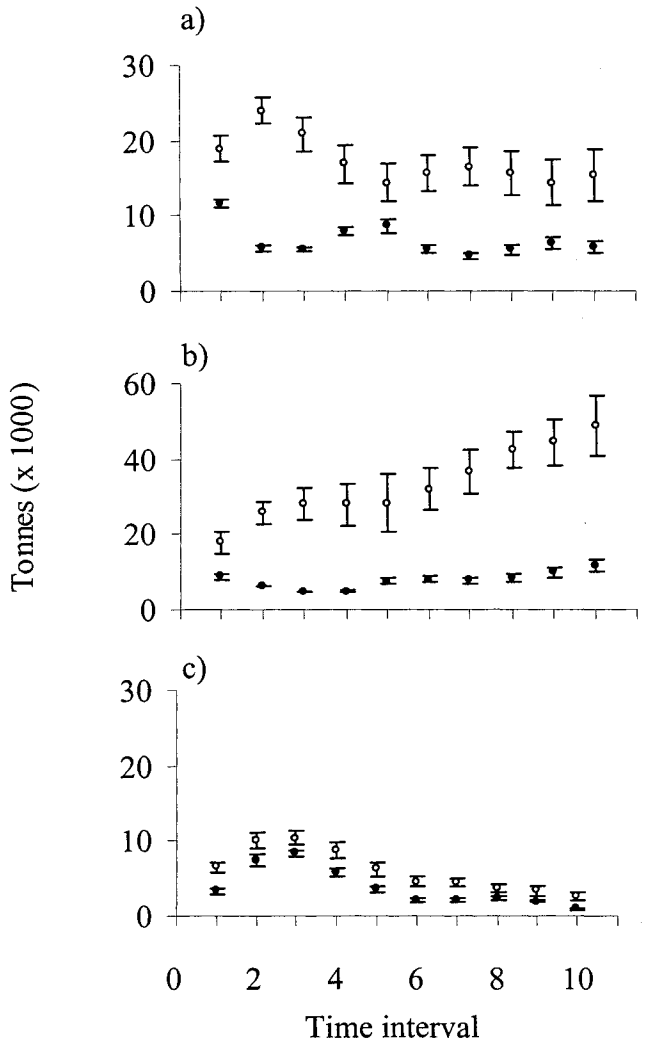

Figure 6.2 Examples of typical temporal trajectories from 20 run simulation (mean ± SD) of cod stock biomass (open circles) and catch (black circles). (a) and (b) represent sustainable fisheries. In (a) there is an initial decline in biomass followed by a steady-state trajectory in both biomass and catch. This fishery targeted cod ages 6-9 (F_2) in scenario S_2, whereas in (b) there is an increase in biomass (S_3) and a steady catch trajectory. F_3 was applied in this example. In (c) a decline trend in both biomass and catch is observed. In this scenario (S_5) cod ages 4-6 were subjected to moderate-high fishing mortality (F_5) through the simulation.

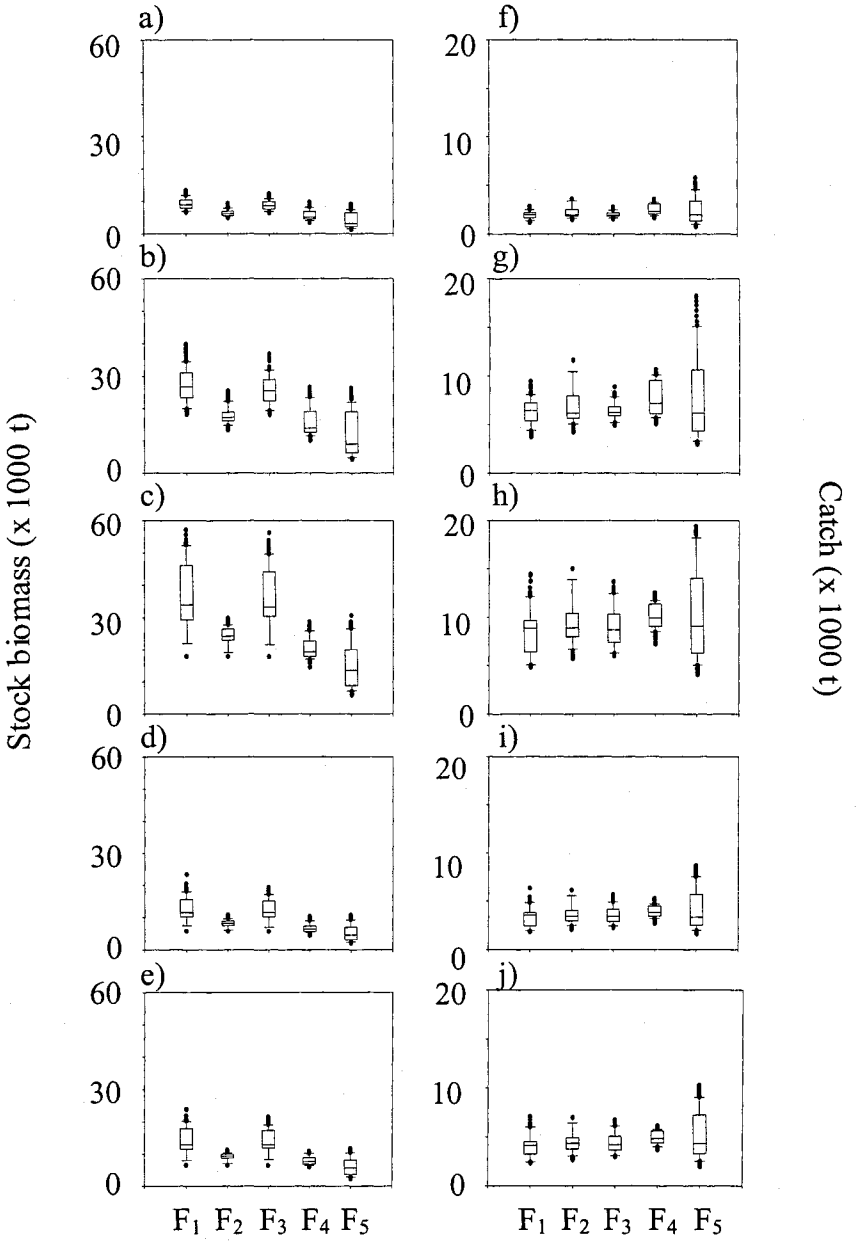

Figure 6.3 Box plots of yearly stock biomass (plots a-e) and corresponding catch projections (plots f-j) from all simulations of the Placentia Bay cod fishery over a 10-year period. S_1-S_5 represent five different stock abundance levels and age composition scenarios and F_1-F_5 different allocations of fishing mortality (Table 6.1). The grey box lower and upper limits represent the 25th and 75th percentiles, the black line inside the box the median and the lower and upper limits of the vertical bars the 10th and 90th percentiles, respectively with values beyond this range represented by black dots.

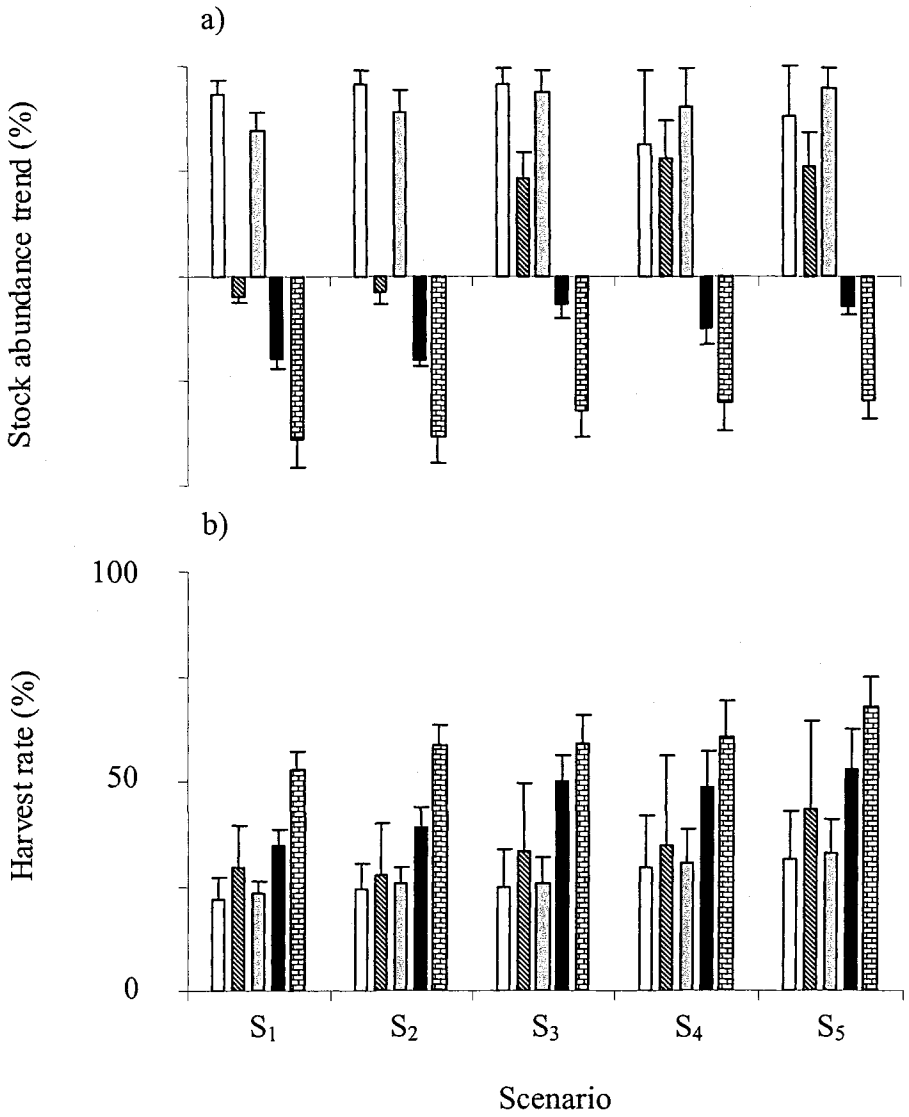

Figure 6.4 Mean trend from 20 run per simulation over a 10-year period in (a) stock abundance (percentage difference between biomass at the beginning and at the end of the simulation) and (b) harvest rate (catch weight/stock biomass) for each scenario (S_1-S_5) and fishing strategy (F_1-F_5). T-bar = one SD. □ = F_1, ▨ = F_2, ▩ = F_3, ■ = F_4 and ▦ = F_5.

Chapter 7 Thesis Summary

This thesis showed that many aspects of seasonal biological cycles of Atlantic cod might potentially impact the effectiveness of management strategies regarding the conservation of stocks and the sustainability and economic benefits from commercial fisheries. Seasonal variability in weight and physiological condition directly influenced the harvested quantities of fish and the economics of the fishery in Placentia Bay, through corresponding variations in product yield and quality. Biological indices such as Fulton's K factor and hepato-somatic index (HSI) were useful in identifying periods of increased stock productivity and yield and could be used as templates for management strategies that would promote fisheries conservation and economic benefits by harvesting fish during periods when biological impacts are minimal and economic returns maximal. As reported in chapter 2, cod stocks from other geographic regions, in addition to many other exploited species inhabiting temperate waters show seasonal variation in weight and/or condition similar to those observed for Placentia Bay cod and hence, in principal, the fisheries on these stocks might also benefit from a harvesting strategy that takes a larger proportion of the catch during periods of peak condition.

In the case of Placentia Bay cod, variability in weight and condition lead to age-specific variability in short term (30-day period) somatic growth, as the result of seasonal changes in the thermal and feeding regimes in the bay, in addition to spawning activity. Minimum and maximum somatic weights for cod ages 4-9 were observed in spring and fall, respectively, with younger cod exhibiting the largest seasonal variation in growth. Large invertebrates (shrimp, crabs) dominated the diet in most seasons, but fish (mainly capelin) was important during late spring and early summer (June-July) when cod

experienced a rapid increase in somatic weight. These findings underline the importance of capelin to cod growth despite cold water temperatures (< 3°C at 50 m) and moderate to high spawning activity. Furthermore, older (larger) cod may enhance growth by carrying out feeding migrations, whereas younger (smaller) fish benefit from local warmer water temperatures. As reported in chapter 3, these findings differed somewhat from seasonal diet findings for other cod stocks on both sides of the North Atlantic Ocean, confirming that cod-prey relationships tend to be stock-specific, with cod being to some extent an opportunistic predator.

Concomitantly with seasonal variability of biological cycles, marked changes in distribution and aggregation patterns of cod were observed in Placentia Bay. Such spatial variability was related to spawning, feeding, overwintering cycles, in addition to migratory patterns and mixing of different groups of cod through the annual cycle and to the complex small-scale bathymetry of the study area. The observed changes in aggregation patterns influenced the precision of fish density indices estimated at different times of the year. These dynamics were investigated through geostatistical modeling of simulated and observed data on cod distribution and abundance, allowing the description and quantification of distribution patterns of cod density in mathematical terms at various scales of observation and the comparison of temporal and spatial changes in density distribution. The conceptual framework developed in chapter 4 is thought to have particular applicability for improving the precision of abundance index estimates of fishes exhibiting gregarious behaviour and biological cycles with strong seasonal components, which include many temperate water species.

Seasonal variations of biological cycles, distribution and mixing of different groups of cod in Placentia Bay resulted in large within-year variations in abundance and of traits such as age and size composition of the stock and impacted current fishing levels on putative stock components and harvest rates during the different fishing seasons. Based on the evidence presented in chapter 5 and reported in earlier studies, it is suggested that Placentia Bay contains at least two groups of cod with seasonal differences in biological traits. A resident group overwinter mostly at the head of the bay and aggregate over the few spawning grounds in springtime and non-resident cod that migrate into the bay, mixing with the local group during the post-spawning period. Between spring and summer, stock abundance increased 4-fold and the age and size composition decreased. By fall most non-resident cod leave the bay and the remaining fish are mostly local non-migratory younger cod, whereas by the end of the fall another group of larger fish is present in the inner bay in dense aggregations and where part of the population overwinter. These complex movements and variability in stock composition and abundance had considerable impact on landings and harvest rates during the study period, with resident and non-resident components of the stock likely being targeted by the fishery in different proportions.

Seasonal variability in stock abundance, age composition and other biological traits caused by migration and mixing of different stock components and other life history characteristics (e.g., feeding and reproductive cycles) resulted in a wide range of abundance levels over time when the stock was subjected to simulated fisheries. The simulations showed that low-moderate fishing mortality resulted in stock growth or

sustainability (i.e., stock conservation and stable catches) over a 10-year period, but moderate-high mortality resulted in abundance decline, particularly when targeting younger fish. The effect of harvest rates on temporal trends of stock biomass was dependent on season and fishing strategy. The simulations also corroborated the findings that the Placentia Bay fishery in 1999 likely over-exploited the largely resident fish present in the fall. The use of simulations provided a useful tool to assist in the development of sustainable harvest strategies.

Regarding fishery management for Placentia Bay cod the most immediate concern would be the potential for overexploitation of the resident component. The approach in management to date has been to extend fishing effort among seasons in the hope of spreading harvest among stock components. Data from simulated fisheries would suggest that the residential stock component alone could sustain a small fishery, particularly if conducted in the fall with low fishing mortality levels applied to all age groups. A fall fishery may also be desirable because cod body condition and growth is highest, leading to better yields and increased profitability to fishers and industry. However, the simulations indicated that regardless of the component targeted it is advisable to allocate effort so that fishing mortality is distributed amongst the broadest range of ages. In fact, promoting the survival of younger fish and allowing age diversity in the stock appears to facilitate good recruitment in Placentia Bay cod (and other regions as well) and hence should be considered by management as possible strategies to promote fisheries conservation of this and other cod stock currently being considered for a limited cod fishery. Information to date indicates that this may be achieved via a fishery using gear

with trap-like selectivity, which tends to harvest a wider range of sizes. Fisheries conducted on spawning aggregations are to be avoided as they are least sustainable, have lower profitability and may disrupt spawning activities.

Based on the work done in this thesis, it is possible to identify some key areas of concern that should be examined before other regions presently under moratorium can be opened to fisheries. Due to the complex spatial and temporal dynamics of stock mixing as observed in Placentia and other areas in Atlantic Canada, there is a need to accurately define and quantify stock components allowing for finer scale management of the fishery. With such knowledge, managers could consider revising the temporal allocation of fishing effort to different components, for example when the greatest diversity in age structure occurs or when a number of stocks (high abundance) are present on the fishing grounds. Therefore before considering opening fisheries in areas where they are presently closed it will be necessary to monitor seasonal changes in stock size and composition to see if mixing occurs. Once a picture of stock movements and availability of different stock components are in place, managers can then consider whether harvesting might best be directed towards a particular season or component and most importantly what harvest rates may be sustained. This could be achieved by simulating fisheries on the documented stock.

In addition, this study suggests that critical life history traits should also be considered when managing cod fisheries. These include periods and areas of increased vulnerability such as during spawning and overwintering, as fish from Placentia Bay and other areas

are usually highly aggregated at these periods and susceptible to both direct and indirect mortalities from fishing. Also since it appears advisable to avoid exploitation of younger fish. Mapping of age/size dependent habitat preferences may aid managers in directing exploitation or protecting specific age groups.

Finally, the results and conclusions of this thesis support the working hypothesis that seasonal biological patterns in cod may be used to develop fishing and management strategies that minimize the impact of harvesting on stock productivity while optimizing economic benefits and other conservation concerns (here mainly the over-exploitation of the resident stock component).